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FACTORS AFFECTING REPRODUCTION OF ENGELMANN SPRUCE [1]

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INTRODUCTION

With the purpose of obtaining much-needed information regarding the laws governing reproduction of Engelmann spruce (*Picea engelmanni*) in the northern Rocky Mountain region, studies were undertaken during the summers of 1920 and 1921 covering representative tracts of cut-over and burned-over land in the spruce type, as well as additional reproducing areas in the natural forest. The areas studied were located in western Montana, in the Blackfeet National Forest. While the data obtained must be regarded as incomplete in many respects, they are of considerable value in view of the great lack up to the present time of sufficient controlled examinations of spruce reproduction, and the far too theoretical conceptions of the requirements for the establishment of the species that have prevailed. Current timber sales on the national forests, as well as the increase in cutting in spruce stands that is now in sight, make imperative a more definite understanding of these requirements, and bring about an urgent demand for data that may be made the basis of timber marking, slash disposal, and selection of logging equipment. As at least a partial response to this demand, the following data and conclusions are submitted.

SEED PRODUCTION

Engelmann spruce is a heavy seed producer. Good crops of cones are produced at intervals of three to four years, while in intermediate years individual trees yield heavy crops of seed. The cones are produced in quantities at the tops of the tree crowns and in the northern Rockies the seed ripens about September 15. Southerly or northerly exposure will hasten or retard ripening about a week. After October 1, seed begin to shed.

The number of seeds average 125,000 per pound for Colorado, 122,400 for Utah, and 190,000 for Montana (3-year average). In past tests, from 0.8 to 1.2 pounds of Montana seed have been extracted from 1 bushel of cones, or at an average rate of 190,000 seeds to the bushel. No data are available on the number of bushels of cones to the acre that a stand of mature trees will produce. It is probable, however, that not less than 3 or 4 bushels per acre are borne by the trees in a good seed year. The quantity of seed thus showered upon the forest floor is very great.

Germination varies widely. Tests at the Savenac Nursery, Lolo National Forest, Montana, indicate that a germination of 50 to 60 per cent is possible. Nevertheless, spruce seedlings are few in number under most natural conditions. Why this should be generally true is a question that can be answered here in part at least. The answer will also serve to indicate the means of obtaining reproduction in logged-off areas.

REPRODUCTION STUDIES

Many of the factors which influence the survival of spruce seedlings are to be seen in the life histories of spruce stands under natural conditions. Although the course of renewal of such stands varies with the zonal position in the spruce type, a general uniformity of reaction to physical conditions is evident. Within the type local variations occur, due to soil, abrupt slopes, or exposure, but these will not affect the conclusions for the type generally.

BURNED-OVER AREAS—UPPER ALTITUDINAL ZONE

A field study of reproduction in the upper altitudinal spruce zone was made

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in the vicinity of Moose Lake in the Big Creek drainage of the Blackfeet National Forest. In 1910 a forest fire swept across a glacial valley below Moose Lake in a northeasterly direction. The site of this burn on both northerly and southerly slopes around Moose Lake furnished an opportunity to study the extent to which spruce and associate species come in on burned surfaces.

The altitude of the valley is 5,000 to 6,500 feet but the study was confined within a range of 5,000 to 6,000 feet. Up to the 6,000-foot contour the stand 12 inches and over in diameter breast high consists of 63 per cent Engelmann spruce and 37 per cent alpine fir (*Abies lasiocarpa*), as shown by the reconnaissance survey for a representative section in this locality. In board foot volume, however, the proportion is 80 per cent for the spruce and 20 per cent for the fir, accounted for by the difference in size of the two species, which yielded, respectively, 7.5 and 16.5 logs per thousand board feet.

On the southerly exposures lodgepole pine (*Pinus contorta*) formed a small percentage of the mixture.

Altitude affects the mixture of the stand noticeably. At about the 6,000-foot contour the spruce ceases to form any considerable portion of the mixture (pl. 1). The alpine fir, however, continues on to higher altitudes and the whitebark pine (*Pinus albicaulis*) replaces the spruce. The stands above 6,000 feet are purely protection forests and are disregarded for the purpose of this report.

The number of surviving seedlings may be considered a reasonable indicator of site conditions. This conclusion is strengthened by an examination of the vegetative cover, of which only the dominant species of plants and shrubs are given below. The thin vegetative cover on the upper southwest slope and the presence of the more drought-resistant species indicate the severity of the site:

Southwest exposure; vegetation (dominant species in order of occurrence):
- Upper slope (13 chains); vegetation very thin—20 to 60 per cent bare soil; soil shaley—
  - Vaccinium membranaceum (?).
  - Xerophyllum tenax.
  - Salix sp.
  - Chamaenerion angustifolium.
  - Amelanchier alnifolia.
  - Acer sp. scattered clumps.
  - Alnus sp.
- Middle slope (13 chains); vegetation thin—10 to 70 per cent bare soil; moisture at lower end of strip—
  - Alnus sp.
  - Salix sp.
  - Chamaenerion angustifolium.
  - Xerophyllum tenax.
  - Pachystima myrsinites.
  - Aquilegia sp.

Southwest exposure—Continued.
- Middle slope—Continued.
  - Acer sp.
  - Populus tremuloides.
- Lower slope (13 chains); vegetation cover thin to dense—
  - Rubus parviflorus.
  - Menziesia glabella.
  - Pachystima myrsinites,
  - Xerophyllum tenax.
  - Vaccinium sp.
  - Acer sp.
  - Salix sp.
  - Ribes sp.

Northeast exposure; vegetation (dominant species in order of occurrence):
- Upper slope (3 chains); vegetation dense to thin—
  - Rubus parviflorus.
  - Menziesia glabella.
  - Chamaenerion angustifolium.
  - Alnus sp.
  - Arnica latifolia.
  - Moss, covering mineral soil.
- Lower slope (8 chains); vegetation very dense, waist-high—
  - Menziesia glabella.
  - Lycopods and moss (under brush cover).
  - Ribes sp.
  - Alnus sp.
  - Vaccinium sp.
  - Arnica latifolia.
  - Acer sp.

As a means of studying the burned area a 55-chain transect was run from the top of one ridge down a southwest slope, across the valley, and up the opposite northeast slope to the top of the opposite ridge. In addition, random sample plots were located at advantageous points.

The transect run in this manner enabled a very satisfactory study of both slopes, and Table I discloses an interesting set of conditions on opposite exposures within the same type. The varying number of seedlings to the acre found on each division of the respective slopes is an index of the complex responsible for the restocking. More seedlings by a large ratio occur on the protected northeastern and lower southwestern slopes. The more moist condition favoring survival is at the same time responsible for a larger seed supply. On these sites, too, a few mature trees escaped the fire; whereas on the upper southwest exposure the drier conditions favored a harder burn and the killing of all the trees (pl. 2, A and B).

Despite the absence of mature living trees within a chain on each side of the transect on the southwest slope, the presence of seedlings less than 5 years old indicates the continuous reseeding of the light-seeded species by wind-blown seed. Scattered trees, particularly on ridges, are doubtless the sources of these seed.

Thus the interruption of the natural course of plant succession by the forest fire has had different effects on the two exposures. As presumably the process of reseeding gave approximately equal opportunity for reproduction over the

The upper limit of the spruce type, Northwestern Montana. Alpine fir and whitebark pine compose the forest cover at altitudes above this

A.—Although no Engelmann spruce seed trees remained alive within a quarter of a mile of this spot, three spruce seedlings are visible, two near the hat and one near the hatchet. This is the top of the ridge near the starting point of the transect. Over the break of the hill to the southwest no spruce seedlings were found. (Moose Lake area)

B.—A very heavy stand of Engelmann spruce and alpine fir seedlings has come in here, on the northeast exposure. Engelmann spruce seedlings were the more numerous of the two on the drier portions of this slope

TABLE I.—*Composition of transect on Moose Lake area, 0.1 chain wide by 55 chains long*

Exposure and slope	Gradient	Seedlings per acre, by species and age classes								Total seedlings per acre	Trees in original stand [b]
		Engelmann spruce		Alpine fir		Lodgepole pine		Miscellaneous species [a]			
		Years		Years		Years		Years			
		0 to 5	6 to 10	0 to 5	6 to 10	0 to 5	6 to 10	0 to 5	6 to 10		
Southwest exposure:	*Per cent*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	
Upper slope (13 chains).	10-40	.....	8	15	62	.....	138	23	.....	246	LPP., AF., WBP., DF.
Middle slope (13 chains).	20-40	8	54	62	216	8	185	15	15	563	AF., ES., DF.
Lower slope (13 chains).	10-40	31	562	23	1,380	.....	154	.....	231	2,381	ES., AF., DF. [c]
Northeast exposure:											
Lower slope (8 chains).	35-75	863	2,840	288	2,300	.....	12	.....	.....	6,303	ES., AF. [d]
Upper slope (8 chains).	10-35	450	2,590	288	4,250	.....	50	.....	37	7,665	ES., AF., WL.

[a] Miscellaneous includes whitebark pine, Douglas fir, and Western larch.
[b] Abbreviations: ES=Engelmann spruce; AF=Alpine fir; WBP=whitebark pine; DF=Douglas fir; WL=Western larch; LPP=lodgepole pine.
[c] Engelmann spruce 14 and 36 inches d. b. h., still alive.
[d] Scattering trees of alpine fir and Engelmann spruce still alive.

entire area, it may be concluded that reproduction of Engelmann spruce can be assured on burned-over areas in the spruce type proper where the soil is favorable to germination and survival and a supply of seed is present. On the southerly exposure above the lower slope, lodgepole pine will first take possession of the site and for a considerable period will be the predominant species. In time the spruce and alpine fir will increase in ratio and, in at least a portion of this type, will eliminate the temporary lodgepole pine. On the northerly exposure, however, a stand of Engelmann spruce and alpine fir will follow immediately.

The importance of taking into full account the influence of exposure on the restocking of spruce stands is here apparent. For example, a selection cut that will give spruce greater advantage over lodgepole pine is indicated for the southerly exposures, while approximately a clean cut will accomplish the same result on the northerly exposures.

IN THE NATURAL FOREST

An examination of the course of reproduction in the openings of the natural forest untouched by fire or by man discloses other factors governing the survival of spruce seedlings, which supplement those found to hold true on the burns. Studies for this purpose were made on 11 sample plots in the Blackfeet National Forest, on which conditions surrounding reproduction were very similar to those following a selection cutting in the spruce–fir type.

Both Engelmann spruce and alpine fir are tolerant species, and form forest stands typically suited to selection cutting when the course of plant succession is permitted to continue long enough without disturbance from outside agencies. Consequently these species are found growing up in openings, and causing the old forest to assume a group composition which is indicative of the manner of renewal (pl. 3, A and B).

The natural reproduction per acre generally found in the spruce–alpine fir mixtures is typified in the following figures from the $\frac{1}{10}$-acre sample plots:[2]

Engelmann spruce, up to 2 inches d. b. h.	96
Engelmann spruce, 3 to 8 inches d. b. h.	64
Alpine fir, up to 2 inches d. b. h.	153
Alpine fir, 3 to 8 inches d. b. h.	151

[2] An investigation in Colorado showed that the Engelmann spruce was more numerous than the alpine fir in the reproduction. HODSON, E. R., and FOSTER, J. H. ENGELMANN SPRUCE IN THE ROCKY MOUNTAINS. U. S. Dept. Agr., Forest Serv. Circ 170, 23 p., 1910.

A.—A view of the manner in which the natural forest renews itself. This selection type of renewal is only possible to the tolerant species—in this case Engelmann spruce

B.—The natural spruce forest. On this divide between Canuck Creek and Ruby Creek, in the Pend Oreille National Forest in northern Idaho, the spruce grows up to 36 inches in diameter, yielding from five to seven 16-foot logs to the tree. The old stand is 90 per cent spruce and 10 per cent alpine fir, but the advance growth is just the reverse, with 90 per cent fir and only 10 per cent spruce

The manner in which this advance growth has come in is significant. The forest floor in these stands is covered by a heavy vegetation made up of *Menziesia glabella, M. ferruginea, Vaccinium* sp., *Pachystima myrsinites, Rubus parviflorus,* and *Arnica* sp.

Tag alder and vine maple (*Acer circinatum*) also occur in clumps in the stand. The duff surface, which is well shaded by the stand and the vegetative cover, consists of a heavy mat of undecomposed and semidecomposed needles, leaves, and twigs in which moss appears occasionally.

Seedlings of alpine fir were found in certain numbers on the duff layer but practically no seedlings of spruce (pl. 4). This lack was strikingly noticeable. Spruce seedlings were found, however, on the mounds of upturned root systems of wind-thrown trees and on decaying, moss-covered logs, especially on decaying logs which were covered with a mat of moss under conditions which favor the growth of twin flower (*Linnaea borealis americana*). Seedlings were also found in the bark scale accumulations around the stumps of trees. The occurrence of spruce seedlings on these surfaces in the green timber appears to hold true generally in the spruce type (pl. 5). The complete explanation of this phenomenon will require additional instrumental study. Present findings indicate, however, that this reproduction, while sufficient to perpetuate a forest following a selection cutting—that is, to supply the natural loss—is not sufficient to restock the stand.

Restocking in the northern Rockies runs predominantly to alpine fir in the natural forest. Alpine fir is, however, disposed to defect to a much greater extent than spruce, and never attains the dimensions of the latter. The reconnaissance data for a typical section of 640 acres show the average number of logs per thousand board feet for spruce to be 7.5 and for alpine fir to be 16.5. Thus stocking after selection cutting has the disadvantage of insufficiency and of favoring the less desirable species.

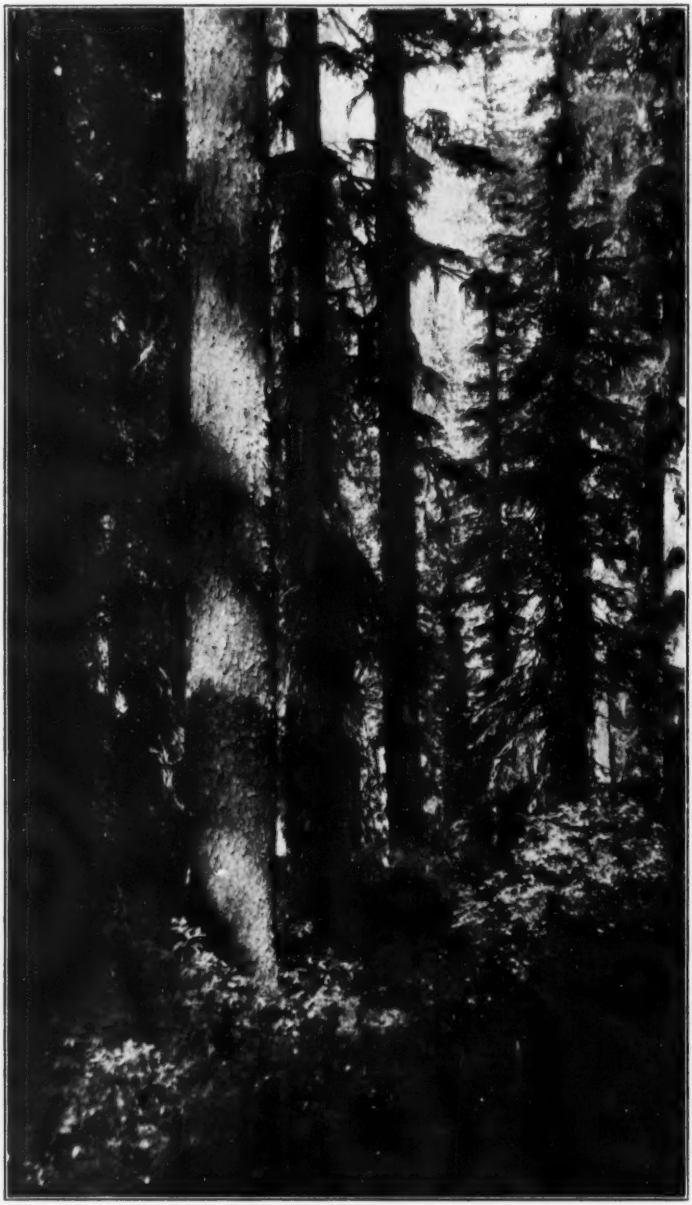
CUT-OVER LAND—MIXED STANDS AT LOWER MARGIN OF TYPE

Old cuttings of timber claims and cuttings along the Great Northern Railway right of way, as well as timber sale cuttings on Nyack and Deerlick Creeks of the Flathead National Forest, Mont., yielded the same conclusions regarding the reproduction of Engelmann spruce as for the natural stands at the higher elevations. The areas studied by sample plots were situated at the lower margin of the spruce type, about Nyack, Mont., on the Great Northern Railway.

TABLE II.—*Detailed observations of occurrence of seedlings in uncut stands or in freshly cut stands at lower margin of type*

Nature of surface	Protection	Engelmann spruce	Alpine fir	Range in age
		Number	*Number*	*Years*
Decaying log covered with moss	Stump shade from south; sarsaparilla, Cornus, and thimbleberry.	4		4 to 9
Decaying stump covered with needles	In shadow of vine maple, fern, and yew	3		5 to 7
Decayed log, now a mound covered with moss and Linnaea.	In shadow of thimbleberry, sarsaparilla, alder, and yew.	42		3 to 10
On humus near the above	In shadow of alder and sarsaparilla	8		2 to 10
10-foot decayed log covered with moss and leaf mold.	In shadow of thimbleberry and sarsaparilla.	32	8	[a] 2 to 10 [b] 2 to 10
Decayed log covered with moss and mold—Linnaea and lycopods.	In shadow of thimbleberry	2	2	[a] 6 to 10 [b] 10
Decayed log covered with moss and leaf mold 1 inch thick.	Shaded only by dense stand overhead	7	4	[a] 7 to 15 [b] 5 to 15
On decayed stump covered with moss and mold.	In shadow of overhead stand	33	3	[a] 3 to 15 [b] 6
On mound of upturned roots 5 feet above ground level; no alpine fir was found here.	In opening of stand; receives direct light about 2 hours in the day.	11		10 to 15
Decayed log stub covered with leaf mold in which twinflower is growing.	In scanty shade of Menziesia and Vaccinium.	9	2	3 to 10

[a] Engelmann spruce. [b] Alpine fir.



An excellent stand of almost pure Engelmann spruce on Big Creek, Blackfeet National Forest. The ground is covered by a dense growth of Menziesia, waist to shoulder high. Under this no reproduction is coming in

Engelmann spruce seedlings growing on the roof of an abandoned cabin. When sufficient protection is given a surface to keep it moist, Engelmann spruce apparently will establish itself and be able to maintain itself for some time almost anywhere

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Table II presents the general manner of occurrence of Engelmann spruce seedlings in the closed natural stands. These observations do not represent the average condition of restocking for the stand, however, for alpine fir occurs on the forest floor more generally than Engelmann spruce, and in a count of advance growth above one foot in height the alpine fir exceeds in numbers. While the advance growth resulting from this manner of renewal has an important part in the restocking following cutting, it is generally insufficient and must be supplemented by a crop of seedlings, which should be predominantly Engelmann spruce. Few seedlings of any species were discovered on the duff layer underneath a heavy cover of vegetation.

In the opening out of a stand as on these cut-over tracts, where fire has not destroyed the surface material, no seedlings such as are described in Table II were found coming in. The full exposure to sun and wind of decayed logs and upturned root mounds renders these locations unfavorable to the survival of either spruce or alpine fir seedlings. A shortage of soil moisture is the very likely explanation, for on an old tree trunk lying half emersed in a mountain lake were found a large number of seedlings of spruce growing in the decaying and broken-down wood, although in full exposure. While the rôle of surface soil moisture will be more fully treated later, it may be said here that restocking in cut-over stands will not occur as it does in uncut natural stands, and that renewal of the forest will therefore depend on favoring natural reproduction in other ways.

SEEDLING SURVIVAL IN CUT-OVER STANDS

In order to obtain data upon seedlings in cut-over stands two drainage areas were studied, Nyack Creek, in the Blackfeet National Forest, and Ruby Creek in the Pend Oreille National Forest.

THE NYACK TRACTS

The Nyack Creek area includes several kinds of treatment. Of these the homestead cuttings, which in this section are 20 years old or older, did not yield representative data because of the influence of grazing. Some portions of more recent cuttings, however, furnished significant evidence.

The first of these tracts is a cutting made in 1911 on which the slash has been left. The tract is flat; the soil is compact of alluvium over a moraine subsoil. A strip 8 chains long was run across the tract to the edge of a broadcast burn. Over a width of 1 chain on this strip a tally of living trees was made, the area totaling 0.8 acre. On a parallel strip 0.1 chain wide, or 0.08 acre, the advance growth was tallied.

TABLE III.—*Composition of reproduction strip on Nyack area* [a]

Species	Standing living trees (0.8 acre)			Restocking advance growth (0.08 acre)	
	Number	Diameters [b]	Rate per acre	Number	Rate per acre
		Inches			
Engelmann spruce	6	8 to 12	7.5	24	300
Alpine fir	2	8 to 10	2.5	20	250
Others	1	8	1	3	38

[a] The original stand consisted of a mixture of Engelmann spruce, Douglas fir, and western larch. The tract is covered with undisposed-of logging slash which is heavy in places.

[b] Diameter at breast height.

Figures for both tallies are given in Table III. The significant fact that came out in the course of these observations is that none of the seedlings found had become established since logging. Those present were on the ground when the stand was cut. This is corroborated by conditions on a sample plot taken in a different area and summarized in Table IV.

TABLE IV.—*Composition of reproduction plot on the Nyack area*

Species	Living trees (0.25 acre)			Advance growth (0.0625 acre)	
	Number	Diameters [a]	Rate per acre	Number	Rate per acre
		Inches			
Engelmann spruce	7	8 to 14	28	16	256
Alpine fir	0	----------	0	36	576
Western larch	2	10 to 14	8	1	16
Others	6	8 to 14	24	2	32

[a] Diameter at breast height.

The stand represented by Table IV is more dense than that represented by Table III, and there is more advance growth on the ground; but the two sample areas agree in respect to the lack of seedlings since cutting. It was

noticeable that in the open spaces between groups of advance growth no seedlings were present even in the absence of a slash cover, notwithstanding the seeds that were without doubt showered upon the ground, for the spruce trees were bearing cones.

Unfavorable surface soil conditions doubtless account for the absence of seedlings. As skidding had been done in the snow and the soil was not broken, an undecomposed duff layer covered the ground. It is also possible that the thin layer of twigs and leaves heated up so much in the sunlight that tender seedlings were unable to survive the heat. However, this can not be said to explain definitely the absence of seedlings, for more needs to be known of the temperatures which exist in this type of soil cover in the critical summer period.

These two tracts furnishing evidences of unsuccessful reproduction following cutting are "flats." The indication is that spruce stands on flats must not be opened out suddenly if spruce reproduction is expected to return immediately in the succeeding stand. To insure the survival of Engelmann spruce, it is better to avoid this condition of wind-swept, dried-out layers of litter.

Tracts on a northerly slope yielded somewhat different results. Reproduction of Engelmann spruce was present in quantities sufficient for a satisfactory stand. Table V presents the findings on four plots selected as representative of the conditions on the northerly exposures.

TABLE V.—*Average distribution of seedlings per acre, by height classes, northerly exposure, Nyack area*

Species	12 inches high and under	Over 1 foot high
	Number	*Number*
Engelmann spruce	512	496
Western larch	224	256
Douglas fir	256	160
Other species	80	96
Total	1,072	1,008

This restocking came in on mineral soil exposed in clearing the right of way for the Great Northern Railway and on burned ground. It is to be noted that Western larch (*Larix occidentalis*) and Douglas fir (*Pseudotsuga taxifolia*) form an important portion of the new growth. The original stand is reflected only partially in the reproduction, for the stumps show the stand to have consisted of a mixture of larch and fir predominantly, and of lodgepole pine, spruce, and alpine fir to a lesser degree. In the reproduction Engelmann spruce appears to be growing better under the more vigorous larch and lodgepole pine saplings. The soil here is covered by a thin layer of larch needles and twigs, which the spruce has evidently found favorable to survival.

Another tract cleared up some of the perplexing features of the reproduction of the Engelmann spruce. This lies also within the Great Northern Railway right of way.

In building the railroad through this region a strip of forest fully 150 feet wide was cleared. The grade was built up with earth scraped out from the sides, and taken from alternate 20 by 20 foot squares along the track. In this manner the unbroken sod extends practically to the grade, save for the ditch, in alternate tongues 20 feet wide. The excavation squares were scraped down from 2 to 3 feet deep. Thirteen of these squares along the track were carefully examined. In all squares spruce seedlings 20 to 25 years old were found. In a few were lodgepole pine and larch seedlings, but no seedlings were found in the grass sod surrounding these excavations. A count showing the stocking of these squares is as follows:

Engelmann spruce, 12 inches high and under	7
Engelmann spruce, over 1 foot high	101
Lodgepole pine, 12 inches and under	0
Lodgepole pine, over 1 foot high	3
Other species	0

The largest trees were from 20 to 25 years old.

Between and beyond these squares, in which the mineral soil had been exposed, the unbroken sod areas extended to the edge of the right of way. On the grass sod no seedlings were to be found. Thus, of these two distinct kinds of surfaces, spruce was coming in at the rate of over 1,500 per acre on the mineral soil, but in the grass not at all. The seed supply for both types of area was of necessity the same. Both areas were exposed to full light and no shade was cast upon either type during the hot hours of the day. The only variables, therefore, were the soil surface and the moisture content.

It may be concluded that the grass sod in this instance used up the soil moisture so completely as to exclude the tree seedlings. This appears to be the key to the problem of the reproduction of Engelmann spruce. The

species has been shown to establish itself even under full light if favorable conditions obtain. These conditions are sufficient moisture to sustain the seedling over the critical dry season, and a mineral soil or moisture-holding surface.

If surface moisture is the deciding factor, the protection of the overstory serves only to prevent desiccation of the soil below the critical point. But vegetation, even under the canopy of a forest, may create unfavorable surface soil conditions, as was noted in the studies in green timber.

Locally it is possible that the chemical contents of the soil, for example acid conditions in poorly drained sites, may preclude the establishment of the spruce, but such areas comprise so small a percentage of the type that in specifying the guiding silvicultural rules this may be omitted from consideration. Such conditions call for detailed investigations of the factors of site controlling reproduction of the species.

Shade may inhibit the restocking of spruce, but to do so it must be very dense, and only in rare instances will the lack of light preclude restocking. In cut-over areas this factor does not operate, and may be dismissed.

The Nyack tracts therefore indicate that where the surface litter is deep and is not broken up in logging, Engelmann spruce seedlings will not survive; nor will they come in in forest openings on flats or other dry sites. On moist mineral soil, however, and on burned-over ground spruce will establish itself; also where forest litter is thin. Grass cover is a dangerous competitor for moisture, and is liable, if not certain, to eliminate Engelmann spruce reproduction. In general, the decisive factor appears to be surface soil moisture available to the seedling during critical periods of the dry season.

THE RUBY CREEK AREA

The Ruby Creek area was cut over in 1917 and 1918 by a varied series of methods, designed to bring out the most favorable form of management for spruce stands. The marking plan prepared by J. Kittredge, jr., in 1916, has been followed throughout with a few modifications. Marking was done to reserve single seed trees, seed trees in groups, in strips, and in blocks. The slash has been uniformly piled and burned, most of the burning being done in 1918.

During the summer of 1921 a field examination was made of the area to ascertain the results of cutting. The method used in the field examination consisted of running strips 0.1 chain wide between groups for reproduction and soil surfaces, and chain-wide strips for standing trees and windfalls. Only on those portions of the tract where trees had been reserved singly and in groups had the logging and slash disposal proceeded sufficiently far to permit drawing any conclusions (pl. 6, A and B). In all, 7 strips 5 to 15 chains in length were run. Of these, 4 strips were on areas where the slash was burned in 1920 and 1921 and so could not yield valid data for definite conclusions, though they will furnish the basis for future comparisons. One strip was run 15 chains from a seed group roughly following the contour on a northwestern exposure with a 20 per cent gradient. The survey of this strip is shown in Table VI.

TABLE VI.—*Reproduction of Engelmann spruce by seedlings and by milacres stocked; Ruby Creek area*

[Basis: Strip 15 chains long by 0.1 chain wide, 150 milacres]

Data obtained	Engelmann spruce			Other species			Totals, all surfaces
	Burned	Mineral	Cover	Burned	Mineral	Cover	
Stocking by species and surfaces:							
Number of seedlings on strip	8	46	12	7	28	13	114
Number per acre of actual area	53	303	80	47	187	87	757
Number per acre of each kind of surface [a]	405	2,300	109	356	1,405	118	
Milacres [b] stocked, by species and surfaces:							
Number of milacres on strip	4	19	10	6	25	10	74
Number per acre	26	127	67	40	166	67	[c] 493

[a] Burned surface, 13.2 per cent of actual area; unburned mineral surface, 13.3 per cent; slash and vegetative cover, 73.5 per cent.

[b] Milacre: A quadrat 6.6 feet by 6.6 feet or 0.001 acre.

[c] The total number of milacres stocked with seedlings of each species is 493, but since more than one species may occur on the same milacre, a smaller number of milacres stocked to all species will result. That number is 413.

A.—A spruce seed group reserved after cutting, Ruby Creek area, Pend Oreille National Forest, Idaho

B.—Single seed trees reserved after cutting. Practically all of the single trees left at this point were blown down. The snow mounds in the picture cover upturned tree roots. The picture is taken on a Ruby Creek cut-over area, Pend Oreille National Forest, Idaho

On the basis of this detailed examination of the sample strip, the surface of the whole area that was burned amounted to 13.2 per cent, the unburned 86.8 per cent. Of the unburned soil surface, mineral soil represented 13.3 per cent of the total area, slash cover 15.2 per cent, and vegetative cover 58.3 per cent. The vegetative cover was classified into three categories according to height, and covered the area as follows: Under 5 inches, 31.5 per cent; 5 to 18 inches, 25.4 per cent; over 18 inches, 1.4 per cent.

The vegetative cover was analyzed in this manner to indicate the extent of the soil covering and the rankness of the vegetative growth. Very few species other than those found on the forest floor in the green timber were noted. Considerable stimulation in growth and increase in number of individuals took place following the cutting. *Tiarella* sp. appeared to be the most prolific and comprised the principal portion in the first group.

The duff layer apparently is a very important factor in spruce reproduction. On the area examined nearly 60 per cent of the tract was covered with litter and duff, and measurements showed that this layer varied from 1 to 3 inches in thickness. The duff is found to be most unfavorable to the establishment of spruce seedlings on cut-over tracts. The spruce seed do not hold over or are not stored in the duff. This is contrary to the behavior of the reproduction of western white pine (*Pinus monticola*) and Douglas fir.

A careful analysis of Table VI will indicate the relative favorableness of the various surfaces to the establishment of the spruce. The burned surface yielded 761 seedlings to the acre, of which 405 were spruce; mineral soil bore 3,705 seedlings to the acre, of which 2,300 were spruce; vegetative and slash-covered surfaces yielded only 227 seedlings per acre, 109 of them spruce.

The burned spots were a disappointment. More seedlings were expected to be found on them. This fact agrees, however, with general observations on spots where slash piles were burned.[3] Apparently the soil is sterilized by the concentrated burn. The absence of weeds and grasses has been noticed, and likewise the absence of seedlings. Further study is needed to explain the consistent absence of seedlings on hard-burned spots for the first five years following the burning. Yet the table indicates that burned surfaces are approximately four times as favorable to seedling establishment as duff or litter.

The mineral soil as represented by skidding trails and by the places where the duff layer is completely decomposed is shown by Table VI to be the most favorable surface for the establishment of spruce seedlings. It is nearly six times as favorable as the burned spots and over twenty times more so than the ground covered with litter and vegetation. This is significant and requires recognition in the treatment of spruce stands.

The important indication of Table VI is the unfavorableness of the litter soil cover to the establishment of spruce seedlings. This is corroborated by the results of a study of germination of Engelmann spruce made in 1921 by J. A. Larsen, shown in Table VII.

TABLE VII.—*Germination and survival of Engelmann spruce in different surfaces*

[2,000 seed sowed in each surface, fall 1920]

Germination and survival, 1921	Ashes	Bare soil	Duff
Germination:			
May 15	0	0	0
May 23	429	641	274
June 6	40	27	4
June 20	10	6	[a]0
July 15	5	15	[a]0
Total	484	689	278
Percentage of germination	24	34	14
Survival:			
Oct. 10	400	524	2
Percentage of survival	83	76	0.7

[a] On the examination dates of June 20 and July 15, practically all the Engelmann spruce seedlings in the duff were dead. Larsen states that the duff layer was 2 inches deep and attributes the failure of the seedlings to inability of the roots to reach mineral soil before they were overtaken by dry conditions.

Study of the Ruby Creek area indicates that reproduction of Engelmann spruce on cut-over areas is dependent on the seeding of the forest floor at the time of or following cutting. Mineral soil surfaces are found to favor the establishment of spruce seedlings by a ratio of more than 20 to 1 over that of duff surfaces. Reproduction on burned spots is not generally so prolific as that on mineral soil.

[3] 45-acre sample plot, Whitman National Forest, Oregon; Seeley Lake sale area, Missoula National Forest, Montana; Beardmore sale area, Kaniksu National Forest, Idaho.

GENERAL CONCLUSIONS

The essential facts controlling the establishment of Engelmann spruce seedlings as shown by these studies may be briefly stated. The conservation of the surface soil moisture throughout the critical dry period is the essential requirement. Reproduction of spruce from seed deposited in the duff can not be depended on under any conditions. Mineral soil surfaces and lightly burned surfaces decisively favor the quick restocking of Engelmann spruce under favorable moisture conditions; but showers of seed over the cut-over tract must be provided for during several years following cutting.

On the basis of these conclusions the following deductions should govern the method of treatment of spruce stands:

Seed trees must be reserved on cut-over areas, despite possibility of windthrow.

The conservation of soil moisture will require an adaptation of cutting and logging methods to the exposure. On southerly exposures a selective type of cutting is required. On northern exposures an approximate clear-cutting may be practical, but with provision for seed supply.

On protected areas as large a percentage as possible of the duff or litter covering of the soil and the native vegetation must be broken up or burned over. This indicates power logging methods and a more general burning over the area than is secured by burning of piled slash. On areas desiccated by sun and wind logging by horses is required.

In all cases the complete control of slash fires is required. On southerly slopes slash must be piled and burned; on protected areas it may be burned in windrows, with adequate control.

A dense vegetative cover will render the soil as critically dry for spruce reproduction as will an exposed situation.

THE RÔLE OF THE HYDROGEN-ION CONCENTRATION ON THE DEVELOPMENT OF PIGMENT IN FUSARIA [1]

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INTRODUCTION

The present investigations are concerned with the influence of the hydrogen-ion concentration of the substratum on the development of pigment by Fusaria.

The production of pigment has been studied by many investigators and this phenomenon has been used as a character for the taxonomic classification of a number of species. Wollenweber (*14*, *15*),[3] Milburn (*5*) and Bessey (*1*) observed that Fusaria produced different colors if grown on either carbohydrates or proteins, each reaction being accompanied by special colors which changed with the change of reactions of the substratum. The chemical nature of the pigment has probably not been studied, nor the factors which govern its development and intensity. The pigment, which is often observed on Fusaria grown in their natural habitat, is pink, the intensity and hues varying with the substratum.

CULTURAL METHODS

The methods employed for the study of the influence of different hydrogen-ion concentrations on the development of pigment by Fusaria, consisted in growing the organism or organisms in culture media at different initial P_H values and observing the color and intensity of the pigment produced therein. As the studies were concerned with the development of pigment at definite hydrogen-ion concentrations, the use of an apparatus which would permit frequent determinations of the hydrogen-ion concentration of the culture solution became essential. The apparatus, used by the writer (*10*) in certain preceding studies was adopted. It provides for frequent determinations of the hydrogen-ion concentration and for the introduction of various volumes of adjusting reagents, for the maintenance of a fairly constant reaction, under relatively aseptic conditions.

The writer (*11*) as well as others found that Fusaria are capable of changing the reaction of their culture media either by increasing or decreasing the hydrogen-ion concentration, the direction of the changes depending on (*a*) the initial P_H value of the culture solution, (*b*) the chemical nature of the nutrient substance, and (*c*) the age of the culture. On account of this ability of Fusaria to change certain of the initial P_H values of their culture media, the different cultures in the experiment were treated in two different ways—some were adjusted to definite hydrogen-ion concentrations with volumes of 0.2 normal HCl or NaOH, and others were left unadjusted. The purpose of this treatment was to distinguish between the influence of the hydrogen-ion concentration of the culture media and that of the hydrogen-ion concentration of the microorganism, namely, that which is produced by the organism and changes the initial reaction of the culture solution during the assimilation of nutrient substances on the development of pigment.

For the growth of the different organisms and the development of pigment, dextrose solutions in combination with certain inorganic salts were used. They were mixed in the following proportion: Distilled water 1,000 c. c., dextrose 20 gm., $MgSO_4$ 2.12 gm., $Ca(NO_3)_3$ 20.71 gm., KH_2PO_4 1.36 gm., and $Fe(NO_3)_3$ 1 c. c. of a 5 per cent solution. Half-liter portions of this solution were adjusted to definite hydrogen-ion concentrations by the addition of appropriate reagents before being placed in the apparatus mentioned, and sterilized. Solid culture media were also prepared by adding to the above 2 per cent agar-agar.

[1] Received for publication July 26, 1924; issued August, 1925.

[2] Now at the University of Hawaii, Honolulu, Hawaii.

[3] Reference is made by number (italic) to "Literature cited," p. 1019.

DEVELOPMENT OF PIGMENT AT DIFFERENT HYDROGEN-ION CONCENTRATIONS

The development of pigment at different hydrogen-ion concentrations was studied concurrently with the changes produced in the initial P_H value of the different cultures by the organisms.

The determination of the particular color of the pigment in the different cultures were made by using Ridgway's Color Standards (*8*) and those of the hydrogen-ion concentrations of the cultures by using Clark and Lub's (*2*) indicators for relatively clear solutions and Hildebrand's (*4*) hydrogen electrode for heavily colored solutions.

Fusarium cromyophthoron Sid. is treated more extensively in these studies than any of the other species of the same genus. With this organism the development of the pigment and nature of the reactions—that is, decreases or increases in the P_H value—are studied in connection with more nutrient substances than dextrose.

ADJUSTED CULTURES

Changes in the initial hydrogen-ion concentration of the cultures of the first set, the adjusted set of cultures, were neutralized with occasional introductions of 0.2 normal HCl or NaOH for the purpose of maintaining constancy in the initial reaction of the culture. The influence of the reactions of the organism on the initial hydrogen-ion concentration of the culture solutions, possibly affecting the development of pigment, is probably eliminated by the introduction of adjusting reagents in the culture media for the neutralization of the resulting changes in the hydrogen-ion concentration. The changes produced in the initial hydrogen-ion concentration of the culture solution were adjusted regularly (in 4-day intervals) by adjusting reagents, according to the instructions of Sideris .[4]

The results which were obtained in connection with the development of pigment by different species of Fusarium are recorded in Table I.

TABLE I.—*Color, intensity, and diffusibility of pigment produced by different species of Fusarium at different hydrogen-ion concentrations, and volumes of adjusting reagents (c. c. 0.2 normal HCl and NaOH) required to maintain the initial P_H value of the solution constant in dextrose solutions*

Organism	Initial P_H	Adjusting reagent		Color of pigment
		HCl	NaOH	
Fusarium cromyophthoron Sid.	3.0	13	0	Pompeian red; madder brown.
Do.	4.0	7	0	Van Dyke red.
Do.	5.0	0	4	Orange pink (diffusible).
Do.	6.0	0	27	Flesh pink.
Do.	7.0	0	90	Shrimp pink.
Do.	7.5	0	120	Colorless.
F. lutulatum Sher.	3.0	10	0	Pomegranate purple.
Do.	4.0	0	4	Pale vinaceous.
Do.	5.0	0	15	Pale orange yellow.
Do.	6.0	0	21	Ivory.
Do.	7.0	0	64	Colorless.
Do.	7.5	0	112	Do.
F. oxysporum Scht.	3.0	10	0	Flesh pink.
Do.	4.0	0	10	Pale vinaceous.
Do.	5.0	0	15	Venetial pink.
Do.	6.0	0	30	Colorless.
Do.	7.0	0	45	Do.
Do.	7.5	0	90	Do.
F. oxysporum var. *longius* Sher.	3.0	17	0	Eugenia red.
Do.	4.0	0	5	Vinaceous.
Do.	5.0	0	13	Shrimp pink.
Do.	6.0	0	25	Colorless.
Do.	7.0	0	70	Do.
Do.	7.5	0	110	Do.
F. sclerostromaton Sid.	3.0	15	0	Acajou red.
Do.	4.0	0	3	Alizarine pink.
F. oxysporum var. *resupinatum* Sher.	3.0	10	0	Jasper pink.
Do.	4.0	0	7	Pale salmon.
Do.	5.0	0	10	Vinaceous lilac.
Do.	6.0	0	20	Flesh pink.
Do.	7.0	0	65	Colorless.

[4] SIDERIS, C. P. THE INFLUENCE OF THE HYDROGEN-ION CONCENTRATION ON THE DEVELOPMENT OF THE PINK ROOT DISEASE OF ONIONS. (3 PARTS) I. THE EFFECT OF THE HYDROGEN-ION CONCENTRATION ON THE DEVELOPMENT OF FUSARIUM CROMYOPHTHORON SID. [Unpublished thesis, Ph. D., Univ. Calif.

TABLE I.—*Color, intensity, and diffusibility of pigment produced by different species of Fusarium at different hydrogen-ion concentrations, and volumes of adjusting reagents (c. c. 0.2 normal HCl and NaOH) required to maintain the initial P_H value of the solution constant in dextrose solutions*—Continued

Organism	Initial P_H	Adjusting reagent		Color of pigment
		HCl	NaOH	
F. redolens Sher.	3.0	12	0	Flesh pink
Do.	4.0	0	4	Flesh pink.
Do.	5.0	0	10	Capucino orange (diffusible).
Do.	6.0	0	30	Colorless.
Do.	7.0	0	60	Do.
Do.	7.5	0	90	Do.
Fusarium sp. (15)	3.0	11	0	Flesh pink.
Do.	4.0	3	0	Do.
Do.	5.0	0	5	Ivory.
Do.	6.0	0	16	Colorless.
Do.	7.0	0	40	Do.
Do.	7.5	0	90	Do.
F. malti Taub.	3.0	15	0	Pale flesh.
Do.	4.0	5	0	Flesh pink.
Do.	5.0	0	4	Cinnamon (diffusible).
Do.	6.0	0	17	Colorless.
Do.	7.0	0	60	Do.
Do.	7.5	0	100	Do.
F. angustum Sher.	3.0	6	0	Flesh pink.
Do.	4.0	0	18	Vinaceous.
Do.	5.0	0	26	Shrimp pink.
Do.	6.0	0	35	Colorless.
Do.	7.0	0	45	Do.
Do.	7.5	0	80	Do.
F. lonchceras Sid.	3.0	6	0	Salmon pale.
Do.	4.0	0	9	Vinaceous, dark.
Do.	5.0	0	20	Shrimp pink.
Do.	6.0	0	35	Colorless.
Do.	7.0	0	70	Do.
Do.	7.5	0	130	Do.
F. culmorum (W. Smith) Sacc.	3.0	16	0	Begonia rose (diffusible).
Do.	4.0	0	3	India red (diffusible).
Do.	5.0	0	6	Victoria Lake (diffusible).
Do.	6.0	0	23	Colorless.
Do.	7.0	0	75	Do.
Do.	7.5	0	120	Do.
F. moniliforme Shel.	3.0	5	0	Flesh (diffusible).
Do.	4.0	0	4	Hydrangia pink (diffusible).
Do.	5.0	0	10	La France pink (diffusible).
Do.	6.0	0	25	Colorless.
Do.	7.0	0	55	Do.
Do.	7.5	0	90	Do.
F. radicicola Wr.	3.0	21	0	Flesh (diffusible).
Do.	4.0	11	0	Scarlet red (diffusible).
Do.	5.0	5	0	Peach red (diffusible).
Do.	6.0	0	31	Colorless.
Do.	7.0	0	75	Do.
Do.	7.5	0	125	Do.
F. martii Ap. et Wr.	3.0	9	0	Apricot orange (diffusible).
Do.	4.0	5	0	Nopal red (diffusible).
Do.	5.0	1	0	Maroon dark (diffusible).
Do.	6.0	0	36	Colorless.
Do.	7.0	0	80	Do.
Do.	7.5	0	130	Do.

EXPLANATION OF RESULTS

The results in Table I indicate that the relative hydrogen-ion concentration of culture media of dextrose solutions is possible to initiate or inhibit the development of pigment in Fusaria. Moreover, the color, intensity, and diffusibility of the pigment may be controlled by the relative hydrogen-ion concentration of the surrounding solution. It becomes evident, therefore, that the ability of the different species to form a certain pigment depends, either wholly or in part, on the relative acidity of the culture media. Concentrations of hydrogen-ion higher than P_H of 3.0 or lower than P_H of 7.0 were found to inhibit the development of pigment, practically, in every case. The optimum hydrogen-ion concentrations for the development of pigment lie between P_H of 4.0 and 5.0.

The nature and extent of the changes produced on the initial P_H value of the different cultures by the Fusaria employed, as they are measured by the volume of the adjusting reagent re-

quired to neutralize them, indicate that the organisms reacted amphoteric at hydrogen-ion concentrations between P_H of 3.0 and 5.0. It means, in other words, that the "isometabolic point," (*11*) or the initial P_H value of the culture solution which is not altered by the reactions of the organism during the utilization or assimilation of dextrose, lies between the P_H values of 3.0 and 5.0. The phenomenon of variation in the biochemical behavior of different species, during the assimilation of different nutrient substances, may serve as a character for the differentiation of groups and possibly of species of Fusarium. It is possible, therefore, when one considers (*a*) the behavior of the different organisms at hydrogen-ion concentrations between P_H of 3.0, 4.0, and 5.0, (*b*) the color and intensity of the pigment, and (*c*) the diffusibility of the pigment, to segregate the Fusaria given in Table I into more or less congenial groups. For instance, *F. cromyophthoron*, *F. redolens* and *F. malli*, may be put in one group; *F. radicicola* and *F. martii*, in another; *F. culmorum* and, possibly, *F. moniliforme*, in another, and all the remaining organisms in one more group.

The behavior of *F. cromyophthoron* in onion decoction does not differ from that in dextrose solutions, except in the position of the P_H value of the "isometabolic point" which lies near or at P_H of 5.0, in onion decoction (Table II).

TABLE II.—*Color and intensity of pigment produced by Fusarium cromyophthoron in onion decoction at different hydrogen-ion concentrations and volume of adjusting reagents required to maintain the P_H value constant during the growth of the organism*

Initial P_H value of culture	Adjusting reagents		Color of pigment
	HCl	Na OH	
3.0	20	0	Phlox purple.
4.0	9	0	Van Dyke red.
5.0	0	1	Orange pink.
6.0	0	15	Colorless.
7.0	0	60	Do.
7.5	0	95	Do.

NONADJUSTED CULTURES

These cultures are concerned with the study of the development of pigment by Fusaria in dextrose solutions whose initial hydrogen-ion concentration was not maintained constant by the introduction of volumes of adjusting reagents. The hydrogen-ion concentration of the culture solution which influences the development of pigment in these cultures is not a constant factor but a variable one. This can easily be explained when one considers that the hydrogen-ion concentration of these cultures is not maintained constant by the addition of adjusting reagents, but is subject to the reactions of the metabolic products of the organism. The pigment, therefore, which is developed under these conditions, is subject to the changes which are produced in the hydrogen-ion concentration of the culture solution by the reactions of the organism with the substratum.

The culture media employed for these studies contained 2 per cent agar-agar. They were solid media, prepared in the manner mentioned previously. The organisms were grown in Petri-dish cultures, containing 20 c. c. of the media.

The observations on the development of pigment were made during the first 12 days' growth of the organism on the above culture media, and are recorded in Table III.

TABLE III.—*Color of the pigment produced by different species of Fusarium at different initial hydrogen-ion concentrations of dextrose-agar cultures, during a 10-day growth*

Organism	Initial P_H	Color of pigment
Fusarium cromyophthoron Sid	4.0	Cinnamon pink.
Do	5.0	Cinnamon.
Do	6.0	Cinnamon purple.
Do	7.0	Vinaceous purple.
Do	7.5	Do.
F. redolens Sher	4.0	Cinnamon pink.
Do	5.0	Cinnamon.
Do	6.0	Cinnamon purple.
Do	7.0	Vinaceous purple.
Do	7.5	Do.
F. malli Taub	4.0	Cinnamon pink.
Do	5.0	Cinnamon.
Do	6.0	Cinnamon purple
Do	7.0	Vinaceous purple.
Do	7.5	Do.
F. lutulatum Sher	4.0	Light vinaceous pink.
Do	5.0	Do.
Do	6.0	Shrimp pink.
Do	7.0	Do.
Do	7.5	Shrimp, pale.
F. oxysporum Scht	4.0	Light vinaceous pink.
Do	5.0	Do.
Do	6.0	Shrimp pink.
Do	7.0	Do.
Do	7.5	Shrimp, pale.
F. oxysporum var. *longious* Sher.	4.0	Light vinaceous pink.
Do	5.0	Do.
Do	6.0	Shrimp pink.
Do	7.0	Do.
Do	7.5	Shrimp, pale.

TABLE III.—*Color of the pigment produced by different species of Fusarium at different initial hydrogen-ion concentrations of dextrose-agar cultures, during a 10-day growth*—Continued

Organism	Initial PH	Color of pigment
F. oxysporum var. *resupinatum* Sher.	4.0	Light vinaceous pink.
Do	5.0	Do.
Do	6.0	Shrimp pink.
Do	7.0	Do.
Do	7.5	Shrimp, pale.
F. sclerostromaton Sid.	4.0	Light vinaceous pink.
Do	5.0	Do.
Do	6.0	Shrimp pink.
Do	7.0	Do.
Do	7.5	Shrimp, pale.
Fusarium sp. (15)	4.0	Light vinaceous pink.
Do	5.0	Do.
Do	6.0	Shrimp pink.
Do	7.0	Do.
Do	7.5	Shrimp, pale.
F. angustum Sher.	4.0	Flesh pink.
Do	5.0	Do.
Do	6.0	Ochraceous buff.
Do	7.0	Do.
Do	7.5	Pale ochraceous buff.
F. lonchceras Sid.	4.0	Flesh pink.
Do	5.0	Pale rose purple.
Do	6.0	Shrimp pink.
Do	7.0	Ochraceous buff.
Do	7.5	Pale ochraceous buff.
F. culmorum (W. Smith) Sacc.	4.0	Hydrangia pink.
Do	5.0	Vinaceous pink.
Do	6.0	Purplish pink.
Do	7.0	Purple.
Do	7.5	Purplish blue.
F. moniliforme (Shel.) Sher.	4.0	Hydrangia pink.
Do	5.0	La France pink.
Do	6.0	Vinaceous pink.
Do	7.0	Vinaceous purple.
Do	7.5	Lilac.
F. radicicola Wr.	4.0	Scarlet.
Do	5.0	Peach red.
Do	6.0	Cinnamon purple.
Do	7.0	Greenish purple.
Do	7.5	Greenish blue.
F. martii Ap. et Wr.	4.0	Maroon red.
Do	5.0	Nopal red.
Do	6.0	Cinnamon purple.
Do	7.0	Greenish purple.
Do	7.5	Greenish blue.

EXPLANATION OF RESULTS

The results given in Tables III, IV, V, and VI indicate that the initial hydrogen-ion concentration of the substratum, if not maintained constant by the addition of adjusting reagents, can not control the initiation or inhibition of pigment, because the reactions produced by the organism during the assimilation of nutrient substances are capable of changing the initial reaction of the culture solution.

Pigment was produced practically in every culture, regardless of the initial hydrogen-ion concentration. It becomes evident, therefore, that the reactions produced by organism or organisms, which, in culture media more acid than the isometabolic point, decreased the hydrogen-ion concentration toward that of the isometabolic point, and in less acid culture media

TABLE IV.—*Color of pigment present in 40-day-old cultures of Fusarium cromyophthoron, grown in dextrose solutions at different initial but nonadjusted hydrogen-ion concentrations, together with determinations of the initial and final P_H value of the different cultures*

Hydrogen-ion concentration of cultures		Color of pigment
Initial P_H	Final P_H	
3.0	4.5	Van Dyke red.
4.0	4.5	Do.
5.0	5.6	Orange pink.
6.0	5.8	Shrimp pink.
7.0	6.2	Pale shrimp pink.
7.5	6.4	Do.

TABLE V.—*Color of pigment present in 40-day-old cultures of Fusarium cromyophthoron, grown in onion decoction at different initial but nonadjusted hydrogen-ion concentrations, together with determinations of the initial and final P_H values of the different cultures*

Hydrogen-ion concentration of cultures		Color of pigment
Initial P_H	Final P_H	
4.0	5.6	Van Dyke, red.
4.7	6.6	Orange pink.
5.4	6.6	Flesh pink.
5.8	6.9	Shrimp pink.
6.2	7.5	Do.
7.3	7.4	Pale shrimp pink.

TABLE VI.—*Color of pigment of sporodochia of Fusarium cromyophthoron, grown on various vegetable tissues*

Vegetable tissues	Color of pigment
Solanum tuberosum L. (tuber).	Pale ochraceous buff to salmon.
Allium cepa L. (bulb)	Pale ochraceous salmon.
Phaseolus vulgaris L. (stems).	Pale ochraceous buff.
Oryza sp. (grains)	Pale ochraceous salmon.
Melilotus alba L. (stems)	Do.

increased it again toward the same point, were responsible for the formation of the favorable hydrogen-ion concentration for the development of pigment. Another interesting phenomenon, in this connection, is the development of different colors of the same pigment at different hydrogen-ion concentrations. At hydrogen-ion concentrations higher or near that of the isometabolic point the majority of the pigments have a reddish-pink color. At hydrogen-ion concentrations, however, lower than that of the isometabolic point, the same pigments, instead of the reddish-pink color, have a purple, blue, yellow, or green color.

The behavior of *Fusarium cromyophthoron* in dextrose solution and onion decoction at different hydrogen-ion concentrations (Tables IV and V) was practically similar to that observed in solid media; that is, pigment was produced at all the different initial hydrogen-ion concentrations between P_H of 3.0 and 7.5. The slight variation in the color of the pigment of the sporodochia of *F. cromyophthoron* (Table VI) is possibly due to the inherent hydrogen-ion concentration or to the difference in the amounts of carbohydrates and proteins contained in the different tissues. If one takes into account the chemical composition of the tissues in its relation to the color produced in the sporodochia of *F. cromyophthoron*, one finds, according to Wehmer (*12*), that the pale ochraceous salmon color is associated with tissues rich in available carbohydrates and the pale ochraceous buff color with those poor in available carbohydrates but somewhat rich in available proteins.

MOVEMENT OF THE REACTIONS IN SOLID MEDIA

These studies are concerned with the movement of the reactions, particularly those of the hydrogen-ion concentration produced by the different organisms, in solid media.

Dextrose agar media were used for the purpose. They were prepared in the manner mentioned in a preceding paragraph. The culture media were tubed in 20 c. c. portions and sensitized with 10 drops of either one of the indicators used for the determination of different hydrogen-ion concentrations, namely, brom phenol blue, methyl red, and brom thymol blue. Inoculations were made with pure cultures of the different Fusaria in slanted media; and the nature, extent, and movement of the changes in the initial hydrogen-ion concentration were examined daily. The initial hydrogen-ion concentration of the culture media at the time of the inoculation was P_H of 5.0. This method was first adopted by Wolf (*13*) and was used in connection with the changes produced in the hydrogen-ion concentration by certain plant pathogenic bacteria. The changes in the hydrogen-ion concentration were determined by the changes in the color of the particular indicator and are recorded in Table VII.

TABLE VII.—*Changes produced on the color of the different indicators by the reactions of metabolic products of the different species of Fusarium on the hydrogen-ion concentration of the culture media*

Organism	Days of growth	Determinations of the changes in the hydrogen-ion concentration		
		Methyl red	Brom phenol blue	Brom thymol blue
Fusarium cromyophthoron		P_H	P_H	P_H
Sid	4	5.0		
Do	6		3.9	
Do	8		4.5	
Do	10			6.8
Do	12			7.2
F. malli Taub	4	5.0		
Do	6		4.0	
Do	8		4.6	
Do	10			6.0
Do	12			7.4
F. lutulatum Sher	4	5.0		
Do	6		4.2	
Do	8		4.6	
Do	10			6.6
Do	12			7.6
F. oxysporum Scht	4	5.0		
Do	6		3.8	
Do	8		4.2	
Do	10	5.4		
Do	12			5.8
F. oxysporum var. *longious* Sher	4	5.0		
Do	6		4.0	
Do	8		4.4	
Do	10			6.6
Do	12			7.4
F. oxysporum var. *resupinatum* Sher	4	5.0		
Do	6		3.8	
Do	8		4.2	
Do	10			6.8
Do	12			7.6
F. angustum Sher	4	5.0		
Do	6		3.6	
Do	8		4.4	
Do	10			6.6
Do	12			7.6
F. loncheceras Sid	4	5.0		
Do	6		3.6	
Do	8		4.4	
Do	10			6.6
Do	12			7.6

TABLE VII.—*Changes produced on the color of the different indicators by the reactions of metabolic products of the different species of Fusarium on the hydrogen-ion concentration of the culture media*—Continued

Organism	Days of growth	Determinations of the changes in the hydrogen-ion concentration		
		Methyl red	Brom phenol blue	Brom thymol blue
		P_H	P_H	P_H
F. culmorum (W. Smith) Sacc.	4	5.0		
Do	6		4.0	
Do	8		4.4	
Do	10			6.0
Do	12			7.0
F. moniliforme (Shel.) Sher	4	5.0		
Do	6		4.6	
Do	8	5.6		
Do	10			6.4
Do	12			7.4
F. radicicola Wr	4	5.0		
Do	6		4.6	
Do	8			6.0
Do	10			6.8
Do	12			7.4
F. martii Ap. et Wr	4	5.0		
Do	6		4.6	
Do	8			5.8
Do	10			6.6
Do	12			7.2

EXPLANATION OF RESULTS

The data in Table VII confirms the results which were obtained on the behavior of Fusarium species in dextrose solutions in all the preceding studies. It is shown that the different organisms increase the hydrogen-ion concentration of the culture media during the utilization of dextrose and decrease it as soon as the supply of this substance is completely removed from the substratum.

The movement of the reactions—that is, the rapidity with which the released hydrogen and hydroxyl ions travel in the different parts of the substratum—is not recorded in Table VII, because the area which manifested the different changes in the hydrogen-ion concentration did not vary in the different cultures. The reactions did not extend much beyond the area which the colony of the different organisms occupied. It may be added that the changes in the color of the indicator, produced by the reactions of the organism in solid culture media contained in test tubes 18 cm. long and 1.5 cm. in diameter, did not extend more than 2 cm. deep from the surface of the colony in the substratum. In cultures, however, older than 20 days the changes in the color of the indicator, and particularly of brom thymol blue, spread throughout the entire culture media. This leads to the conclusion that both the hydrogen and the hydroxyl ions, released in the substratum by the reactions of the organism with the nutrient substances, do not travel fast in solid culture media, because, if they did, the reactions of the hydrogen ions as well as the changes in the color of the indicator would be instantaneous.

Methyl red was far less sensitive than any of the other two indicators. It did not change color after the growth of the organism, this reaction possibly being due to some modification of the methyl red molecule by the metabolic products of the organism.

BEHAVIOR OF DIFFUSIBLE PIGMENTS IN ACIDS AND ALKALIES

The object of these studies was to explain some of the reactions, produced in solid media by certain Fusarium species, which tend to induce the development of pigment of different colors at different hydrogen-ion concentrations.

Diffusible pigments of certain Fusarium species, produced at P_H of 4.0 and 5.0 in dextrose solutions whose initial hydrogen-ion concentration was maintained constant by the addition of adjusting reagents, were treated with 0.1 normal NaOH. The determinations were made with 9 c. c. of the solution containing the diffused pigment against 1 c. c. of the reagent. The changes which were produced in the color of the pigment are recorded in Table VIII.

TABLE VIII.—*Changes produced in the original color of the pigment of certain Fusarium species by the addition of 0.1 normal NaOH*

Organism	Initial P_H	Color of pigment before treatment	Color of pigment after treatment
Fusarium culmorum	5.0	Victoria lake	Dusky auricula purple.
F. radicicola	4.0	Scarlet red	Lilac.
F. martii	5.0	Maroon, dark	Matheus purple.
F. malli	5.0	Cinnamon	Light vinaceous purple.

EXPLANATION OF RESULTS

The results given in Table VIII indicate that the pigment, produced at P_H of 4.0 and 5.0 by certain Fusarium species, if brought in contact with free hydroxyl ions, changes color from reddish pink to blue, green, lilac, or purple. Therefore the blue, green, and purple colors of the pigments of certain Fusarium species, produced at P_H of 7.0 and 7.5, were due to the influence of the hydroxyl ions of the culture media. It becomes evident, from a consideration of the results obtained in the different studies, that the organism or organisms produce the chromogens necessary for the development of pigment at hydrogen-ion concentrations between P_H of 3.5 and 5.5 and that the different colors which are formed from the chromogens later on depend on the hydrogen-ion concentration of the culture media. The mechanism by which these organisms bring about the appropriate reactions in the culture media for the development of chromogens and the formation of pigment of different colors is discussed to a certain extent in the preceding pages and more extensively in a different publication of the writer (*11*).

GENERAL DISCUSSION

The pigments produced by Fusaria belong possibly to the same class of pigments which are produced from chromogens named by Palladin (*6*) "*respiration chromogens.*" According to the same author, these chromogens are glucosides soluble in water and upon the addition of peroxidase and hydrogen peroxide produce red (rarely lilac or violet) color which might change with further oxidation to a dark violet or black. Rupe (*9*) found that an alkaline solution of these chromogens absorbs oxygen very actively, and Combes (*3*) found that the transformation of the chromogen into the pigment is accompanied by increased respiratory activity. Palladin and L'vov (*7*) are of the opinion that these chromogens serve as acceptors of hydrogen. Moreover, they state that they were able to retard the process of alcoholic fermentation by employing the respiration pigment of the white beet to remove the active hydrogen as it was formed.

The pigments produced by Fusaria and those attributed by Palladin to respiration chromogens have certain reactions in common. Both are formed from chromogens during a very active respiration, absorb oxygen very rapidly in alkaline solutions; and are red or pink in acid solutions, and violet, purple, or blue in alkaline solutions.

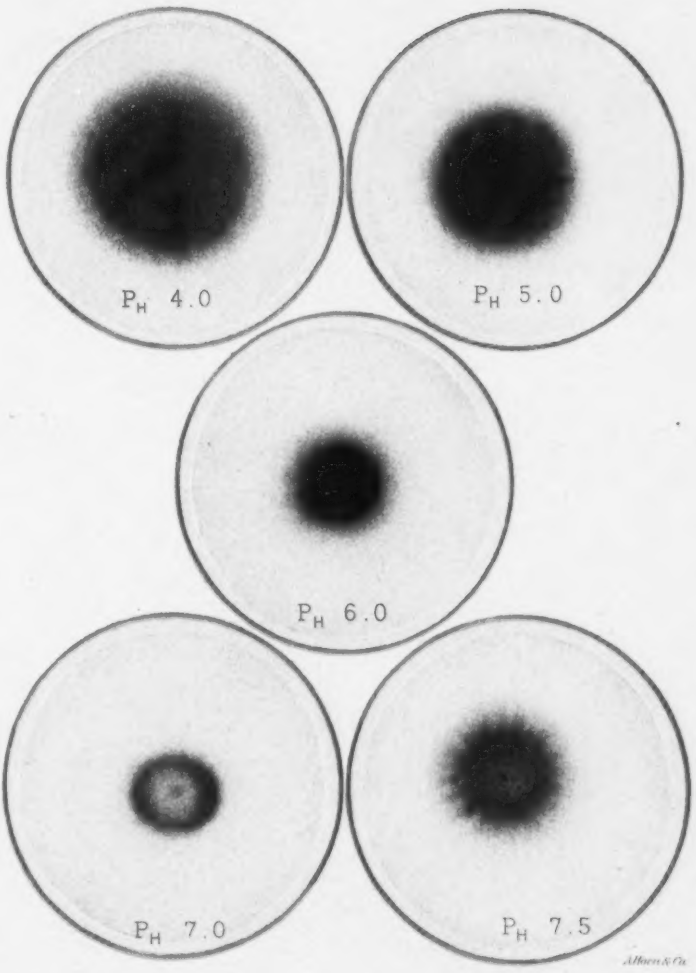
The series of reactions which initiate the development of pigment, during the assimilation of certain nutrient substances by Fusaria, are possibly produced as follows: The organisms, in culture media whose hydrogen-ion concentration is not appropriate for the development of chromogens, may or may not change the initial reaction of the culture media either by increasing or decreasing the hydrogen-ion concentration with their metabolic products. Then, if the hydrogen-ion concentration of the surrounding culture solution is favorable for the development of chromogens, the organisms may produce these substances the color of which in acid solutions may be red, vinaceous, or pink, and in alkaline solutions violet, lilac, purple, blue, or green.

Carbohydrates are essential for the development of pigments. The rôle which they play, in this respect, is not known exactly. They may supply the substances (glucose and organic acids) for the synthesis of glucosides, particularly of the chromogen-glucoside, or the organic acids for the restoration of an hydrogen-ion concentration appropriate for the development of chromogens. The development of chromogens is definitely controlled by the hydrogen-ion concentration of the surrounding solution. In dextrose solutions chromogens may be produced in cultures whose hydrogen-ion concentration is maintained constant by the addition of adjusting reagents at P_H between 3.5 and 5.5, but not above or below these values.

Plate 1 shows the different colors of the pigment produced by *Fusarium culmorum* (W. Smith) Sacc. in solid media at different hydrogen-ion concentrations. The colors from acid to alkali change from red to blue. The chromogen for the blue pigment at P_H 7.5 and the purple at P_H 7.0 was not produced at the above hydrogen-ion concentrations, but at such hydrogen-ion concentrations as were created by the organic acids produced by the organism during the utilization of dextrose. It is possible for the organism, in solid media, to produce a local acidity or alkalinity, that is, a reaction which does not spread throughout the entire culture medium but is confined

EXPLANATORY LEGEND FOR PLATE 1

Fusarium culmorum, grown in solid media at different hydrogen-ion concentrations, namely, P_H 4.0, 5.0, 6.0, 7.0, and 7.5


P_H 4.0
P_H 5.0
P_H 6.0
P_H 7.0
P_H 7.5

to the area covered by the colony of the organism, because the movement of the hydrogen ions or hydroxyl ions is very slow and the time required for their neutralization is relatively long. It is easy to see how, with the development of a local reaction, one with a P_H between 4.0 and 5.5 appropriate for the formation of chromogens is possible. The blue color of the pigment produced in alkaline cultures is due to oxidation which is accelerated by the presence of free hydroxyl ions in the surrounding solution.

SUMMARY

The development of pigment by Fusaria is mainly controlled by the hydrogen-ion concentration of the culture media.

Pigment was produced practically by all the different species employed in these studies in dextrose solutions at hydrogen-ion concentrations between P_H 3.5 and 5.5, where the initial P_H value was maintained constant by the addition of adjusting reagents. In cultures, however, whose hydrogen-ion concentration was not maintained constant, pigment was produced at P_H 3.0, 4.0, 5.0, 6.0, 7.0, and 7.5.

The pigment may be of two kinds: Diffusible and nondiffusible, that is, pigment retained within the cell and pigment escaping through the plasmatic membrane and cell wall.

The color which a pigment may take depends on the hydrogen-ion concentration of the surrounding culture solution.

The movement of the hydrogen ions and hydroxyl ions released by the reaction of the metabolic products of Fusaria through solid culture media is very slow.

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EFFECT OF SEEDS UPON HYDROGEN-ION CONCENTRATION EQUILIBRIUM IN SOLUTION [1]

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INTRODUCTION

In an earlier paper [2] it was shown that the hydrogen-ion concentration of alkaline salt solutions in which seeds were immersed had changed markedly after about 15 hours of imbibition. The P_H changes recorded were all in one direction, namely, towards the acid side, and appeared to be fairly definite for each species of seed. The conclusion was drawn that these reaction changes were directly related to ion-absorption by the seeds.

The object of this paper is to show the rate of reaction changes and the existence of a definite equilibrium in solutions which have been in contact with seeds.

EXPERIMENTAL DATA

In view of the fact that a marked difference exists in the absorbing power of seeds of different species (seeds of the leguminous type show higher rates of absorption than seeds of the gramineous species [3]), four kinds of large seeds were selected, as follows: Corn (*Zea mays*), lupine (*Lupinus albus*), beans (*Phaseolus vulgaris*), and soy beans (*Soja maxima*).

The representative salt solutions, mineral and organic acids, covering the range of acids and salt radicles, are given in the tables. In the case of the mineral and organic acids an effort was made to bring the different acids to a dilution giving approximately a reaction of P_H 3.0. Some of the acids could be secured only at a nominal per cent and it was thought best to state the dilution in P_H values instead of in terms of normality. A large number of different salts were tried, but, for the comparison of the radicles, the representative potassium salts are selected and only two chlorides with other bases are entered in the tables.

Fifty seeds of each species were placed in small bottles each containing 100 c. c. of solution; 1.8 c. c. of this solution was pipetted off after definite time intervals, and the hydrogen-ion concentration of the solution was determined by the colorimetric method. The results of these determinations are given in the tables as the averages of at least two trials. In Tables I, II, and III the initial P_H values are compared with the readings at different intervals.

The rate of reaction change is not the same for all salt solutions, although a certain equilibrium is reached in the solutions after the seeds have been immersed sufficiently long (Table I). Corn changed the reaction of KCl to a point of equilibrium in about 15 minutes, while 15 hours were necessary in the case of K_2SO_4. For the mineral and organic acids similar differences were observed.

For mineral and organic acid solutions, considerably more time was necessary to reach the point of equilibrium than for salt solutions (Tables II and III.) On account of the rapid increase in the strength of the acids with every increment of the P_H values, a longer time for the reaction changes could be expected. Nevertheless, all acid solutions which had been in contact with the seeds after a certain period of time reached the same point of equilibrium as the salt solutions.

The P_H values observed in oxalic acid and potassium chloride solutions (corn and beans) plotted against time in minutes are presented in Figure 1. The curves show a fairly rapid rise during the first few time intervals with a flattening out toward the point of equilibrium. Ordinarily the solutions remain at this point indefinitely, but slight changes can be brought about by an increase of temperature. This explains why some of the salt solutions show slightly different P_H

[1] Received for publication Aug. 8, 1924; issued August, 1925. Paper No. 177 of the Journal series, New Jersey Agricultural Experiment Station, Department of Soil Chemistry and Bacteriology.

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TABLE I.—*Reaction changes in representative salt solutions*

Time	K_2SO_4		K_2HPO_4		KNO_3		$KClO_3$		$CaCl_2$	
	Beans	Corn	Beans	Corn	Beans	Corn	Beans	Corn	Beans	Corn
	P_H	P_H	P_H	P_H	P_H	P_H	P_H	P_H	P_H	P_H
Initial	5.9	5.9	4.1	4.1	5.4	5.4	6.5	6.4	6.0	6.0
After 30 sec	5.9	5.9	4.1	4.1	5.3	5.3	6.5	6.2	5.9	5.9
After 1 min	5.9	5.7	4.2	4.2	5.5	5.1	6.5	6.1	5.8	5.7
After 2 mins	5.9	5.5	4.2	4.2	5.5	5.2	6.5	5.7	5.8	5.6
After 3 mins	5.9	5.3	4.2	4.1	5.6	5.2	6.5	5.7	5.7	5.6
After 5 mins	6.0	5.4	4.0	4.1	5.7	5.4	6.3	5.4	5.9	5.6
After 10 mins	6.0	5.3	4.1	4.1	5.6	5.1	5.9	5.3	5.9	5.4
After 15 mins	6.0	5.2	4.0	4.0	5.6	4.9	5.9	5.1	5.9	5.4
After 20 mins	6.0	5.0	4.2	4.3	5.7	4.8	5.7	5.1	5.8	5.3
After 30 mins	6.0	5.1	4.4	4.3	5.7	4.8	5.7	5.0	5.8	5.3
After 1 hr	6.0	5.1	4.4	4.3	5.8	4.7	5.7	4.9	5.7	5.3
After 2 hrs	5.9	4.9	4.8	4.5	5.8	4.7	-------	4.9	5.6	5.0
After 15 hrs	5.4	4.2	5.4	4.2	5.9	4.3	5.7	4.2	5.5	4.1
After 48 hrs	5.4	4.2	5.4	4.1	5.8	4.2	5.7	4.0	5.5	4.0

TABLE II.—*Reaction changes in mineral acid solutions*

Time	H_2SO_4		HCl		HNO_3		50 per cent H_3PO_4		H_3BO_3		KCl		$BaCl_2$	
	Beans	Corn	Beans	Corn	Beans	Corn	Beans	Corn	Beans	Corn	Beans	Corn	Beans	Corn
	P_H	P_H	P_H	P_H	P_H	P_H	P_H	P_H	P_H	P_H	P_H	P_H	P_H	P_H
Initial	3.0	3.0	3.0	3.0	3.0	3.0	3.0	3.0	5.5	5.5	6.7	6.7	5.9	5.9
After 30 sec	3.1	3.0	3.1	3.0	3.0	3.0	3.1	3.0	5.7	5.4	6.6	6.4	5.9	5.8
After 1 min	3.1	3.0	3.3	3.1	3.1	3.0	3.5	3.0	5.9	5.3	6.5	6.1	5.9	5.6
After 2 min	3.2	3.1	3.5	3.2	3.2	3.1	4.4	3.1	6.0	5.3	6.5	5.2	5.9	5.5
After 3 min	3.2	3.1	3.6	3.2	3.3	3.1	4.5	3.1	6.2	5.3	6.5	4.9	5.9	5.4
After 5 min	3.3	3.1	4.0	3.2	3.5	3.1	4.7	3.1	6.3	5.2	6.3	4.6	5.9	5.3
After 10 min	4.1	3.1	4.6	3.3	3.6	3.2	5.2	3.2	6.4	5.1	6.2	4.1	5.9	5.2
After 15 min	4.6	3.1	4.9	3.4	3.8	3.3	5.7	3.2	6.6	5.1	6.2	4.0	5.9	5.0
After 20 min	4.7	3.1	5.2	3.4	3.9	3.3	5.7	3.5	6.5	4.9	6.1	4.0	5.9	4.6
After 30 min	5.1	3.2	5.5	3.4	4.0	3.3	5.8	3.7	6.5	4.7	5.9	3.9	5.9	4.3
After 1 hr	5.4	3.3	5.7	3.4	4.6	3.3	5.9	4.5	6.4	4.6	5.6	4.0	5.9	4.1
After 2 hrs	5.6	3.4	5.8	3.9	5.4	3.4	5.9	4.4	6.2	4.3	5.7	3.9	5.7	4.1
After 15 hrs	5.8	3.7	5.9	3.9	5.8	3.8	5.9	4.2	6.1	4.2	5.5	3.9	5.5	4.1
After 40 hrs	5.9	3.9	5.8	4.1	5.8	3.9	5.9	4.1	5.9	4.1	5.4	3.9	5.4	4.1

TABLE III.—*Reaction changes in representative organic acids*

Time	Bibasic acid		Hydroxy acids				Fatty acids				Amino acid		Aromatic acid	
	Oxalic		Citric		Lactic		Formic		Acetic		Asparagin		Benzoic	
	Corn	Beans	Corn	Beans	Corn	Beans	Corn	Beans	Corn	Beans	Corn	Beans	Corn	Beans
	P_H	P_H	P_H	P_H	P_H	P_H	P_H	P_H	P_H	P_H	P_H	P_H	P_H	P_H
Initial	2.9	2.9	2.9	2.9	3.0	3.0	2.9	2.9	2.9	2.9	3.7	3.7	3.2	3.2
After 30 sec	2.9	3.0	2.9	2.9	3.0	3.0	2.9	3.0	2.9	2.9	3.7	3.7	3.3	3.5
After 1 min	3.0	3.1	3.0	3.0	3.0	3.1	3.0	3.1	2.9	2.9	3.7	3.7	3.5	3.7
After 2 min	3.1	3.2	3.0	3.1	3.1	3.1	3.1	3.2	2.8	2.8	3.7	3.8	3.6	3.7
After 3 min	3.1	3.4	3.0	3.1	3.1	3.1	3.1	3.4	2.9	2.8	3.8	3.8	3.6	3.7
After 5 min	3.3	3.9	3.0	3.2	3.1	3.2	3.2	3.6	3.0	3.0	3.8	3.8	3.6	3.9
After 10 min	3.6	4.2	3.0	3.3	3.1	3.6	3.3	4.4	3.0	3.0	3.9	3.8	3.7	4.3
After 15 min	3.7	4.5	3.1	3.7	3.1	3.9	3.5	4.7	3.0	3.0	3.9	3.8	3.7	4.5
After 20 min	3.8	4.8	3.1	3.9	3.1	4.0	3.5	4.9	3.0	3.1	3.9	3.9	3.6	4.6
After 30 min	3.9	5.1	3.1	4.2	3.1	4.2	3.6	5.4	3.1	3.3	4.1	4.0	3.7	4.8
After 1 hr	4.0	5.4	3.2	4.6	3.3	4.5	3.9	5.5	3.1	3.5	4.1	4.4	3.9	5.2
After 2 hrs	4.0	5.6	3.5	4.9	4.0	5.5	4.1	5.8	3.1	3.7	4.2	5.3	3.9	5.5
After 15 hrs	4.1	5.8	3.9	5.7	4.1	5.8	4.1	5.9	3.4	4.2	4.1	5.8	4.0	5.8

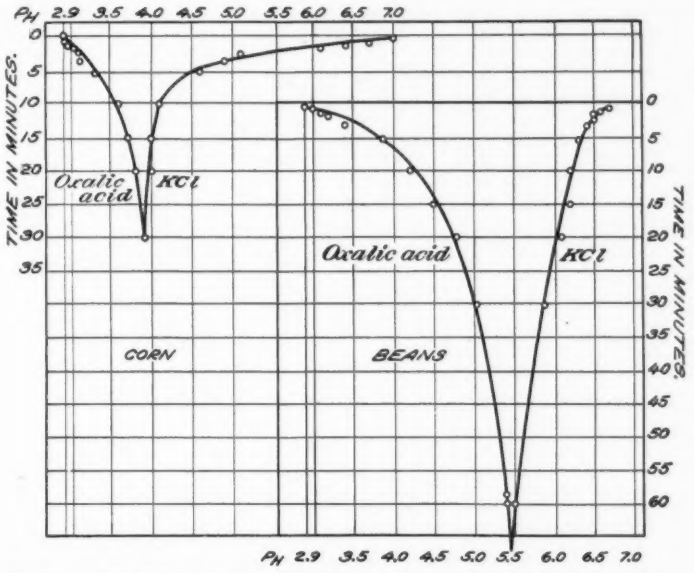

FIG. 1.—Chart showing the P_H values observed in oxalic acid and potassium chloride solutions (corn and beans) plotted against time

values upon standing when the temperature varies. Because variations in temperature cause apparent variations in ion absorption the question might be raised whether or not this is due to the comparative dryness of the seeds at the time of immersion. If the seeds are dry, water intake would presumably be greater and occur at a faster rate than when wet seeds are used. To test this point corn seeds were soaked for a certain period in distilled water before submersion into potassium sulphate. After the immersion a fresh potassium sulphate solution was used again to see when the limit of ion intake was reached. Table IV gives some of the data secured. It will be noticed that the changes produced by previously soaked seeds were very similar to the changes in the case of the air-dry seeds. The same seeds were then quickly taken out of the solution and again placed in a KCl solution of 7 atmospheres osmotic pressure. The observed changes of reaction were not as rapid and extensive as was the case during the first immersion. After 15 minutes the initial P_H value of 5.9 was changed to 5.0 and had risen again after 60 minutes to P_H 5.3. Immersion of these seeds in the same and in fresh solutions for 15 hours caused no further changes. There seems to be no doubt that the equilibrium was reached. Previous soaking in water seemed to have no influence as far as ion intake is concerned.

TABLE IV.—*Corn seeds soaked in distilled water for 30 minutes before submersion into potassium sulphate*

Time	K_2SO_4 (7 atm.)	Fresh solution	Time	K_2SO_4 (7 atm.)	Fresh solution
Minutes	P_H	P_H	*Minutes*	P_H	P_H
Initial	5.9	5.9	After 20	4.1	5.2
After 5	5.1	5.3	After 30	4.3	5.2
After 10	4.9	5.1	After 45	4.2	5.2
After 15	4.3	5.0	After 60	4.2	5.3

After the reaction changes were observed, the first impulse was to hold responsible the rapid changes of life phenomena in the dormant seed when brought in contact with the solutions, or possibly the action of enzymes which are characteristic during the processes of germination. The possibility of changing the salt solutions and acids at such a rate by these agents seemed remote; but, to make sure, seeds were killed by subjection to a temperature of 100° to 102° C. for periods of 48 and 96 hours. To prevent all possibility of enzyme action, beans were subjected to similar temperatures and then placed in formaldehyde. The data secured for seeds dried for 48 hours are given in Table V.

TABLE V.—*Reaction changes in solutions in which "fresh" and dried seed were soaked. The dried seeds were subjected to a temperature of 100° to 102° C. for a period of 48 hours*

Time	NaCl				KCl				Formic aldehyde	
	Lupine		Corn		Lupine		Corn		Beans	
	Fresh	Dried	Fresh	Dried	Fresh	Dried	Fresh	Dried	Fresh	Dried
	P_H	P_H	P_H	P_H	P_H	P_H	P_H	P_H	P_H	P_H
Initial	6.6	6.6	6.6	6.6	6.7	6.7	6.7	6.7	3.6	3.6
After 30 sec	6.6	6.6	6.6	6.6	6.5	6.5	6.4	6.5	3.7	3.6
After 1 min	6.5	6.5	6.3	6.5	6.5	6.3	6.1	6.3	3.8	3.6
After 2 min	6.5	6.5	6.1	6.2	6.5	6.3	5.1	6.3	3.8	3.6
After 3 min	6.5	6.3	5.6	5.8	6.5	6.3	4.9	5.9	3.9	3.6
After 5 min	6.3	6.3	5.4	5.7	6.3	6.3	4.5	5.5	4.0	3.7
After 10 min	6.3	6.3	4.9	4.9	6.3	6.3	4.1	4.9	4.3	3.9
After 15 min	6.3	6.3	4.6	4.4	6.2	6.3	4.0	4.7	4.5	4.1
After 20 min	6.3	6.3	4.4	4.3	6.3	6.1	4.0	4.2	4.7	4.4
After 30 min	5.9	6.2	4.1	4.1	5.9	6.1	3.9	4.1	4.9	4.8
After 1 hr	5.5	6.3	4.1	4.1	5.5	6.1	3.9	3.9	5.0	4.9
After 2 hrs	4.9	4.9	----	----	4.9	5.2	----	----	5.4	5.3
After 18 hrs	4.7	4.6	----	----	4.7	4.6	----	----	----	----

A study of this table shows that the reaction changes were possibly somewhat slower in the dried seeds but that in general the reaction velocity did not undergo great changes. It might be that because of the drying of the seeds, slight chemical changes occured in the seed, so that the mechanical intake of the ions was retarded; or it might be that, on account of the drying, some of the retained moisture in the seeds was driven out and the moisture content had to be replaced to its original amount before the seeds were able to absorb the ions from the salt solutions and acids. It is interesting to note, however, that in all cases the final equilibrium was established regardless of the previous drying. Even in the case of dried seeds soaked in a formaldehyde solution the hydrogen-ion concentration was changed from P_H 3.6 to P_H 5.3 after 2 hours. None of the dried seeds germinated, while from 61 to 84 per cent of the "fresh" seeds germinated after being subjected to immersion in salt solutions for 2 hours.

It is known that when dry seeds are placed in moist soil or salt solutions they absorb moisture with great power. This absorption is not a simple phenomenon but implies forces like imbibition, capillarity, surface tension, osmotic pressure from internal salts, and possibly other forces. The amount of absorption depends on the salt concentration in the soil or solution. In previous papers [4] it has been shown that there is a difference in the absorbing powers of different species of seeds, that different salt solutions are differently affected, and also that there is variation in the amounts of salt solutions (in the form of ions) taken up by the different seeds.

Loeb [5] has suggested that in amphotheric membranes like those in the protoplasm of root hairs, and of vacuolate cells generally, the opposite sides of the membrane may be oppositely charged. Many different kinds of membranes are semipermeable and the property of all in common in that they are colloidal gels. Water can penetrate both phases of the colloidal gel, but salt molecules attempting to penetrate the membrane would be prevented by physical phenomena. From the data here presented, it seems clear that the ions of the solutions are rapidly absorbed by the seeds, but the material which makes up the seeds, and especially the seed coats, can not directly be compared with the colloidal gel or the semipermeable membrane of the cells of root hairs.

A study was therefore conducted to determine what part of the seed plays the most important rôle in ion ab-

[4] RUDOLFS, W. EFFECT OF SALT SOLUTIONS HAVING DEFINITE OSMOTIC CONCENTRATION VALUES UPON ABSORPTION BY SEEDS. Soil Sci. 11: 277-293, illus. 1921.
——— EFFECT OF SEEDS UPON HYDROGEN-ION CONCENTRATION OF SOLUTIONS. Bot. Gaz. 74: 215-220. 1922.

[5] LOEB, J. THE REVERSAL OF THE SIGN OF THE CHARGE OF MEMBRANES BY HYDROGEN IONS. Jour. Gen. Physiol. 2: 577-594, illus. 1920.

sorption. The seed coats of soy beans were carefully removed from the cotyledons and both cotyledons and coats placed in different acids and salt solutions; similar material was placed in distilled water. The water was not redistilled and was, as usual, slightly acid. The figures secured for beans soaked in hydrochloric acid are presented in Table VI.

TABLE VI.—*Reaction changes in 0.001 normal HCl and distilled water caused by dicotyledons of soy beans*

Time	HCl		Water	
	Coats	Dicotyledons	Coats	Dicotyledons
	P_H	P_H	P_H	P_H
Initial	3.6	3.6	6.6	6.6
After 30 sec	4.7	5.0	6.6	6.6
After 1 min	4.8	5.4	6.6	6.6
After 2 min	5.2	5.7	6.6	6.6
After 3 min	5.3	5.9	6.6	6.7
After 5 min	5.5	6.0		
After 10 min	5.6	6.0	6.7	6.6
After 15 min	5.9	6.1		
After 20 min	6.0	6.1	6.6	6.6
After 30 min	6.1	6.1	6.6	6.6
After 60 min	6.1	6.1	6.6	6.6

It can be seen at once that the cotyledons of the soy beans were more powerful in absorbing ions from this acid than were the coats. No reaction changes seemed to occur in distilled water. The dicotyledons of soy beans contain saturated acids, great amounts of oil and masses of protein. Since proteins are amphotheric, it seems justifiable to assume that the proteins are mainly active in ion absorption. It is well known that carbohydrates do not behave in a way similar to proteins. However, the influence of corn seed coats, the carbohydrates of the inner cells of the seeds, and pure starch upon the reaction changes of magnesium sulphate solutions as compared with redistilled water was determined. Table VII gives the condensed data secured in one series of trials.

The reaction changes brought about by the seed coats in the $MgSO_4$ solutions were similar to the reaction changes caused by the whole seeds, while the reaction changes caused by the endosperm of the corn seeds (carbohydrates mainly) were negligible. As could be expected, no changes occurred in the salt solutions or water with pure starch. The protein content of the corn seed coat seemed, therefore, responsible for the changes of hydrogen-ion concentrations.

It may perhaps be said that the characteristic external acidity which each species of seeds tends to preserve seems to be determined by the chemical properties of its chief constituent protein. The fact that a given species of seeds causes (and maintains in weak solutions) a certain equilibrium of hydrogen-ion concentration might possibly throw some light upon the question why certain plants are better able to withstand an acid or alkaline soil than others. If for instance a certain species of seeds maintains a characteristic P_H point 4.0, the seedling possibly would be able to survive in a more acid soil than a species of seeds with a characteristic P_H point of 5.8. However, a certain equilibrium caused by the seeds in the surrounding nutrient or soil solution does not necessarily mean that the growing plant causes a similar reaction, because the watery protein materials in the growing plant cell might have different characteristic P_H points. Moreover, the growing plant seems to be able to adjust or regulate internal changes readily. This is shown by Bauer and Haas,[6] who

TABLE VII.—*Influence of corn seed coats and starch upon the reaction of changes of magnesium sulphate as compared with distilled water*

Time	$MgSO_4$		Water		Pure starch	
	Coats	Endosperm	Coats	Endosperm	$MgSO_4$	Water
	P_H	P_H	P_H	P_H	P_H	P_H
Initial	6.7	6.7	7.0	7.0	6.7	7.0
After 15 min	4.6	6.7	6.9	6.9	6.7	7.0
After 30 min	4.2	6.6	6.9	6.9	6.7	7.0
After 60 min	4.2	6.5	6.8	6.9	6.7	7.0

[6] BAUER, F. C., and HAAS, A. R. C. THE EFFECT OF LIME, LEACHING, FORM OF PHOSPHATE AND NITROGEN SALT ON PLANT AND SOIL ACIDITY, AND THE RELATION OF THESE TO THE FEEDING POWER OF THE PLANT. Soil Sci. 13: 461–477, illus. 1922.

state: "In the case of the soy bean roots, while the hydrogen-ion concentration usually showed a direct relation to the acidity of the soil, the total acidity (of the plant) usually varied in the opposite direction. The data of these experiments strikingly show the power possessed by plants to regulate internal acidity. Marked differences in the acidity of the soil caused only small differences in the acidity of the plant juices." It might be that the acidity or alkalinity of soils as such is not always the limiting factor in soil productivity. It is recognized that the measure of soil acidity alone may be useful in determining the amount of lime necessary to adjust a soil for a crop, but the establishment of the characteristic P_H point for the seeds as revealed in these tests together with the determination of the hydrogen-ion concentration of the soil solution might serve as a better indicator in the use of particular crops in particular soils.

SUMMARY

When seeds were immersed in representative salt solutions, mineral and organic acids, and the changes in hydrogen-ion concentration and reaction changes were recorded, it was found that different seeds are able to change the hydrogen-ion concentration of the solutions to definite points, and that certain equilibrium is reached in all solutions after the seeds have been immersed sufficiently long. The changes of the solutions in which previously soaked seeds were immersed are very similar to the changes in solutions caused by air-dry seeds.

The reaction caused by dried seeds (dried at 100° to 102° C. for 48 and 96 hours) are similar to the reaction changes caused by fresh seeds, although the rate of reaction is slightly less. The cotyledons of soy beans were more powerful to absorb ions from the solutions than were the seed coats; and the reaction changes caused by seed coats of corn were similar to the changes brought about by the whole seeds, while changes caused by the endosperm of the seeds (carbohydrates mainly) were negligible. The chemical properties of the chief protein constituent of the seeds seem responsible for the changes in hydrogen-ion concentrations of the solutions.

FUSARIUM RESISTANT CABBAGE: PROGRESS WITH SECOND EARLY VARIETIES[1]

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INTRODUCTION

About 25 years ago E. F. Smith (*7*),[2] while studying the bacterial black-rot disease of cabbage, recorded another disease which he correctly diagnosed as caused by a vascular Fusarium. In this connection he pointed out the serious danger from this and similar soil-borne fusarial diseases. Apparently this disease was not then widespread in its occurrence and little further attention was given to it until about 10 years later. Then Harter (*2*) noted its serious development in the southeastern States and Manns (*6*) reported it as becoming highly destructive in the intensive cabbage-growing districts of Ohio. It was about this time that the senior writer learned that the cabbage growers along the shores of Lake Michigan from Milwaukee southward into the environs of Chicago were being forced out of the cabbage industry because of the rapidly increasing inroads of this "yellows" disease and sent a culture of the fungus to Wollenweber (*10*), who described and named the species *Fusarium conglutinans.*

Since then evidence has rapidly accumulated to show that this parasite has become established across the continent to California on the west and to the Gulf States on the south. Its occurrence from Iowa and southern Minnesota across the northern States to southern New York has been a matter of frequent report for several years. It was found by Walker to be destructive near Mobile, Ala., in 1918, and in 1923 H. D. Barker, in correspondence, reported it as serious in central Mississippi. In 1922 Monteith observed it on kale at Santa Rosa, Calif.; in 1923 Walker observed it in the Greeley district of Colorado, causing a 25 per cent loss in one field; and Stokdyk (*8*) has reported it from Kansas.

Moreover, in accord with Smith's warning, wherever introduced it has soon become the most seriously destructive of all cabbage diseases in those regions where climatic conditions favor its development. It has, however, been further shown (*1, 8, 9*) that this disease, like most of those caused by vascular Fusaria, is distinctly limited by soil-temperature relations. It is a high-temperature parasite, and since the invasion occurs only through the root system when the soil temperature remains below about 17° C. its attacks are inhibited, whereas above this temperature the severity of the disease increases rapidly with rise in temperature for about 10°. These temperature influences are especially potent in the northern States during the earlier growth of the plant when it is relatively shallow-rooted, the periods of most serious susceptibility being (*a*) the seedling stage and (*b*) the time immediately following transplantation.

Previous publications (*3, 4*) have demonstrated the practicability of controlling this disease through the selection of disease-resisting strains and have recorded the earlier successes with certain of these as used locally in the vicinity of Racine, Wis., and Chicago, Ill. More recent developments have confirmed the earlier judgments as to the futility of turning to any other method of control of the cabbage Fusarium disease. At the same time they have indicated the pressing and widespread national importance of developing and of securing the adequate maintenance of disease-resisting strains. At first it seemed that perhaps two or three such strains of different types would meet the outstanding needs.

[1] Received for publication July 29, 1924; issued August, 1925. The writers wish to acknowledge the assistance of W. B. Tisdale, now of the Florida experiment station, who was associated with this work from 1919 to 1922, and of E. C. Tims, who assisted in the conducting of field trials in 1922 and 1923 and has conducted other investigations of the problem to be reported in an independent publication entitled, "Studies on the Fusarium Disease of Cabbage" (Ph. D. thesis, Univ. of Wis., 1924). Appreciation is also expressed to the National Kraut Packers' Association for generous financial support, and to Martin Meeter, chairman of the seed committee of that association, for his hearty cooperation.

[2] Reference is made by number (italic) to "Literature cited," p. 1034.

This was upon the assumption that the disease was localized. Now that it is recognized as essentially national in its distribution, urgent appeals are coming from the several commercial cabbage-growing interests for a correspondingly diversified range of types to meet their various local or regional needs.

This publication is presented as a report of progress since the date of the last detailed article (*4*) in the writers' efforts to meet these needs. In order to link the present publication with the former, it will be necessary to state briefly the place now held by the previously distributed resistant strains and to review their behavior under commercial conditions.

PRESENT STATUS OF RESISTANT STRAINS PREVIOUSLY DISTRIBUTED

At the time of the last detailed publication (*4*) there were two strains of the Ball Head or Hollander type of winter or storage cabbage. Of these the first was distributed as Wisconsin Hollander, but upon the subsequent development of an earlier selection was renamed Late Wisconsin Hollander in order to distinguish it from the other, which was named the Early Wisconsin Hollander. This earlier, shorter-stemmed strain was selected from the parent Wisconsin Hollander strain by W. J. Hansche, an expert cabbage grower and dealer of Racine.

In addition to these two resistant strains of the winter or storage cabbage, two other resistant strains of cabbage of the mid-season or domestic type had been obtained. These were distributed under the names Wisconsin All Seasons and Wisconsin Brunswick. Efforts with these four strains during the past five years have been directed primarily toward the guidance of those interested or engaged in the commercial growing and distribution of seed. Trials on sick soil have been made annually, using either seed of these resistant strains from stocks grown by Wisconsin farmers or similar seed from stocks of the commercial seed trade which had been secured by increasing the Wisconsin resistant stock through growing it for one generation in one or another of the commercial seed-growing sections.

During this period no noticeable deviation or loss in resistance in any of these strains has been found where the seed was grown successively from heads selected from sick soil. Nor has any appreciable reversion been noted where such seed is increased properly for a single generation in a yellows-free commercial seed region. The effect of repeated multiplication in a disease-free area is not known, but it is to be expected that it would in time lead to considerable loss in resistance through the reproduction of a small but probably increasing percentage of susceptible plants (*5*).

Through the development of the four above-named varieties, the leading demands for resistant strains of late storage and medium late domestic cabbage have been met. Through succeeding years reselection of these varieties should continue by those interested, and from them special strains adapted to various localities should result. As noted above, this has already occurred in the selection of the Early Wisconsin Hollander at Racine by Hansche; and independently of this work Bugner, of Chicago, has selected another resistant strain of Hollander which is now offered in trade channels. In the same way further selection and possible improvement by others should naturally proceed with these later varieties. The writers' attention since 1919 has been directed toward the development of resistant strains from earlier varieties of cabbage to meet the needs of kraut manufacturers and cabbage growers in general.

SELECTIONS FROM SECOND-EARLY VARIETIES

Using the methods already described, the selection was started in 1919 from two standard second-early types—one a flat-head type, the other a round-head type. For the first the standard variety All Head Early was used as the original stock; and for the second, two very similar varieties, Glory of Enkhuizen and Copenhagen Market. The All Head Early is some two weeks earlier than All Seasons, is not as rank and leafy a plant as the latter, and produces a somewhat flatter head. The Glory of Enkhuizen requires about the same length of season as All Head Early, has fewer outer leaves than All Seasons, and produces a prominent spherical head. The original Copenhagen Market was of the same general type as Glory of Enkhuizen, but somewhat earlier. There are now so many strains of the Copenhagen Market, however, that the two names are used more or less interchangeably. At least the strains of both varieties with which the writers have worked are so similar that it will probably not be advisable to carry them farther as distinct varieties. None of these selec-

tions have the extreme earliness of certain Copenhagen strains, but are in line with later strains of this variety and with the generally accepted Glory of Enkhuizen type.

The writers have had to contend with greater practical difficulties inherent in methods of handling the early varieties as compared with the late-season varieties. These results from the fact that in the first place, in order to secure evidence as to both relative disease resistance and horticultural type, the plants must be brought to maturity in late summer rather than autumn; and in the second place, plants matured so early, especially those of the earlier soft types, do not keep well in winter storage. Many of the selections in the early years of the work were lost during winter storage, and this loss was naturally most severe with the earlier maturing individuals.

During the last three years this difficulty has been overcome to a considerable degree in two ways. In the first place, the resistant plants, after having passed the severe yellows period in midsummer and having sufficiently approached maturity to permit of critical selection for earliness and type, are "lifted" from time to time sufficiently to break part of the root system and thus delay final maturation. They can thus be allowed to remain in the field, under Wisconsin conditions, until freezing weather, when winter cabbage is naturally placed in storage. By thus shortening the storage period, greater success is insured. In the second place, a small number of the best heads, after six to eight weeks of dormancy in the field or in storage, are planted in the greenhouse, where with proper handling a seed crop may be matured in May and June. The latter method has the especial advantage of making it possible to try out the new strains immediately. It also has the advantage of facilitating hand pollination both for selfing and crossing.

SELECTIONS FROM ALL HEAD EARLY

Two series of selections from All Head Early have been carried through the second generation. The original stock in each case was from a lot of seed grown by Linnaeus Allen at Cutchogue, Long Island. The original selections of the first series were made from a thoroughly sick field at Union Grove, Wis., in 1919. The second series was selected from rows grown in trial plots at Racine, Wis., in 1920. The behavior of the resulting strains on sick soil at Racine is summarized in Table I. In each season's trials there was included for comparative purposes a susceptible commercial strain of the variety and the Wisconsin All Seasons, which is one of the most highly resistant types. The trials extended over the years 1921 to 1923. Some variation between the seasons in the severity of yellows is evident. Judging from the behavior of the commercial strain and of Wisconsin All Seasons, the year 1921 afforded the severest test, while that of 1923 was perhaps the least severe. It is well to keep this point in mind in comparing the behavior of the different series reported.

Heavy mortality of seed plants reduced the trials in Series I to a single strain in each generation. It will be seen from the data in Table I that considerable resistance was already shown in the first generation (XL–20–1 (pl. 1, A), though it was not equal to Wisconsin All Seasons. Of the selections from this lot, only one seed plant survived, and, having grown in isolation, it was probably self-pollinated. In the trial of this strain (XL–22–1) no yellows whatever was found in a large population, although a trace of the disease might have resulted in a warmer season (pl. 1, B). The plants in this trial were unusually uniform, but unfortunately they deviated so widely from the characteristic All Head Early type as to be of little value. They were of a yellowish green rather than the characteristic dark green color; the heads matured much later than All Head Early, and had a decided tendency to become peaked as they matured This example illustrates the great danger of rapid digression from the desired type in the selection of cabbage which, being normally cross-pollinated, is probably homozygous in few if any of its characters.

In the second series less rapid advance in the acquisition of resistance was made. All strains showed a high percentage of yellows in the Broesch plot and somewhat less in the Drummond plot. The difference in disease occurrence between the two plots is probably due to the fact that two types of soil are represented, which may vary somewhat as to temperature as well as other factors. From the five first-generation strains tried, one (XL–21–5) was picked for further selection, since it developed the best type of plant, while it was nearly equal to XL–21–4 and superior to the other strains in resistance. Of the 26 heads selected from XL–21–5, four plants produced seed in the greenhouse, and these

TABLE I.—*Behavior of selections from All Head Early cabbage when grown on yellows-sick soil at Racine, Wis.*

Series No.	Generation	Strain No.[a]	Year mother head selected	Year seed grown	Year strain tested	Behavior on affected soil						Remarks
						Broesch plot			Drummond plot			
						Total plant	Per cent yellows	Per cent headed	Total plants	Per cent yellows	Per cent headed	
I	First	XL–20–1	1919	1920	1921				69	33	68	5 heads selected.
		Wisc. All Seasons							135	18	84	
		Commercial All Head Early.							135	99	0	
	Second	XL–22–1	1921	1922	1923	507	0	92	934			Decidedly off type.
		Wisc. All Seasons				258	1	83				
		Commercial All Head Early.				213	90	15	138	72	12	
II	First	XL–21–1	1920	1921	1922	157	75	22	18	44	55	Discarded.
		XL–21–2				231	69	42	215	58	70	Do.
		XL–21–3				245	66	47	121	48	82	Do.
		XL–21–4				263	64	22	121	25	94	Do.
		XL–21–5				265	71	47	120	34	94	26 heads selected.
		Wisc. All Seasons				364	8	96	119	3	99	
		Commercial All Head Early.				105	77	12	142	75	42	
	Second	XL–23–1	1922	[b]1923	1923	113	41	44				Good; discarded.
		XL–23–2				91	32	62				Type good; preserved.
		XL–23–3				63	22	66				
		XL–23–4				49	20	73				Very good type; preserved.
		Wisc. All Seasons				258	1	83				
		Commercial All Head Early.				213	90	15				

[a] The method used in numbering the cabbage strains is as follows: A Roman numeral has been used consistently throughout the trials to designate the original commercial variety from which the selection was made, XL being this numeral for All Head Early. The pair of Arabic figures next appearing, i. e., between the dashes (–21–, etc.), indicates the year (1921, etc.) when the seed was grown, and the last figures is the number of the particular strain in question.

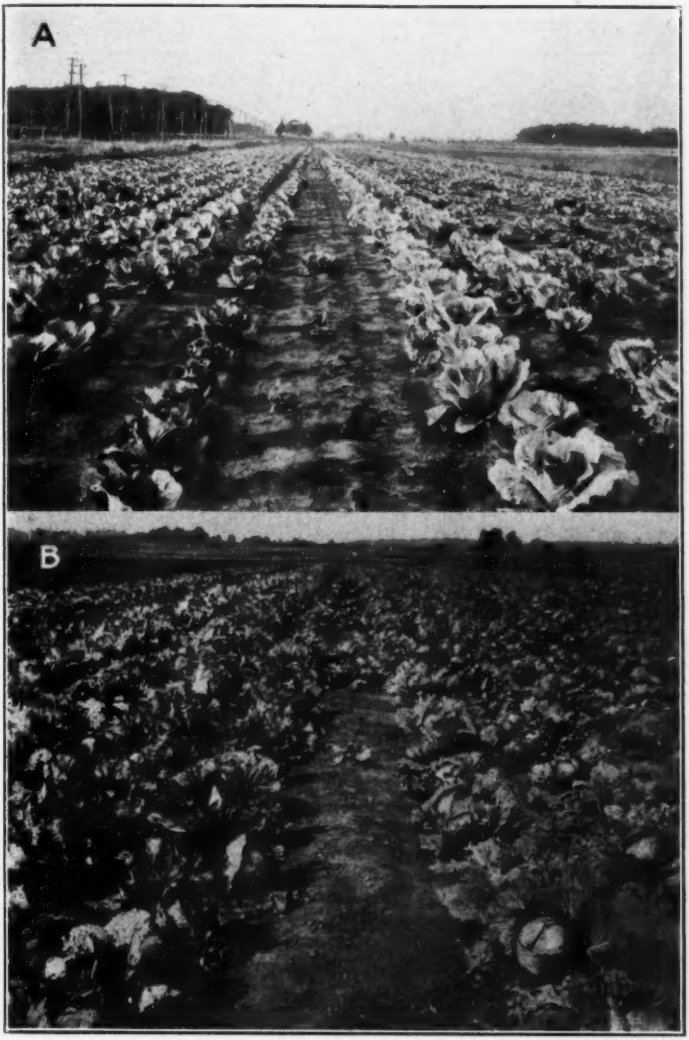
[b] Seed was greenhouse grown.

second generation strains were tried out in 1923. A considerable improvement in resistance was shown by these strains, and contrary to the results in Series I, the type was quite satisfactory (pl. 1, B). Strain XL–23–1 was discarded because of its poor resistance, but the remaining three were preserved for further selection.

SELECTIONS FROM THE GLORY–COPENHAGEN TYPE

Four separate series of selections have been made from the Glory-Copenhagen type. The results of the work to date are summarized in Table II. In each case the original selections were made from plantings of the standard variety on very sick soil, either in commercial fields or from experimental trial plots. Series I was selected from a commercial field at Union Grove, Wis.; Series II and III were selected from commercial rows in the trial plots at Racine, Wis.; and Series IV was selected from commercial rows in a demonstration plot conducted by F. D. Fromme at Marion, Va.

Trials on sick soil with seed from the first-generation selections have been made in each case. In every trial a commercial strain of Glory of Enkhuizen and a strain of Wisconsin All Seasons were included. These trials extended over the years 1921 to 1923, and the variation between these seasons in the severity of yellows is again to be noted. In no case have any of the first generation strains equaled the Wisconsin All Seasons in resistance. On the other hand, it will be seen by comparison that a marked advance has been made over the commercial strain in the first selection. In fact, the strains in Series III and IV are at a point where as such they are of distinct commercial value.



TRIALS OF SELECTIONS FROM ALL HEAD EARLY ON YELLOWS-SICK SOIL

A. View of Drummond plot, Racine, Wis., in 1921. The row in the center was planted with commercial All Head Early; note that the yellows disease has killed nearly every plant. The next row to the left is a *first generation* selection from All Head Early, XL–20–1. Note the nearly complete stand as compared to the control. The remaining rows to the left are the resistant Late Wisconsin Hollander. The first two rows to the right of the control are strains of the resistant Maryland Flat Dutch

B. View of the Broesch plot, Racine, Wis., in 1923. The row in the center is commercial All Head Early; note that here, as in field A, this is nearly destroyed by disease. The first row at the left of the control is the progeny of a single plant (XL–22–1) selected from the All Head Early selection, XL–20–1, tried in 1921 and shown above in A. The second generation selection proved to be highly resistant, but is of undesirable type, being too late in maturity, too peaked as to head shape, and too yellowish green as to color. The first row on the right of the control contains second-generation selections from All Head Early (XL–23–1 to 5), belonging to a line distinct from those noted above. These strains are also highly resistant and approximate more closely the desired type. These give promise of commercial value

TRIALS OF SELECTIONS FROM GLORY OF ENKHUIZEN-COPENHAGEN MARKET TYPE UPON YELLOWS-SICK SOIL

A. View of Drummond plot, Racine, Wis., in 1923. The row at right center is commercial Glory of Enkhuizen; note that the yellows disease has killed most of the plants. The four rows at the left are first generation selections (XXX-22-1 to 4) which are highly resistant

B. View of the Broesch plot, Racine, Wis., in 1923. The control row in the center is commercial Glory of Enkhuizen, which suffered badly from disease. The several rows at the right are of the same first generation selections shown in A (Series IV, XXX-22-1 to 6). At the left are first generation selections of Series III, XXXV-21-1 to 6. Note that in each case the selected strains show high degrees of resistance as compared with the commercial control of the same variety

TABLE II.—*Behavior of selections from Glory of Enkhuizen–Copenhagen Market strains of cabbage when grown on yellows-sick soil at Racine, Wis.*

Series No.	Generation	Strain No.	Year mother head selected	Year seed grown	Year strain tested	Behavior on affected soil						Remarks
						Broesch plot			Drummond plot			
						Total plants	Per cent yellows	Per cent headed	Total plants	Per cent yellows	Per cent headed	
I	-------	Commercial Glory	------	------	1921				260	98	2	
	-------	Wisc. All Seasons	------	------					135	18	84	
	First	XXXV–20–1 [a]	1919	1920					288	43	56	Poor; discarded.
		XXXV–20–4							184	42	64	Fairly good type; preserved.
II	-------	Commercial Glory	------	------	1922	123	92	27	123	82	37	
	-------	Wisc. All Seasons	------	------		364	8	96	------	------	------	
	First	XXXV–21–1	1920	1921		128	30	70	11	27	95	Fairly good type; preserved.
III	First	XXXV–22–1	1921	1922	1923	246	16	72	737	17	67	Poor type; discarded.
		XXXV–22–2				254	18	72	925	19	68	
		XXXV–22–3				255	20	75	555	17	76	
		XXXV–22–4				254	14	80	632	16	73	Good type; preserved for further selection.
		XXXV–22–5				257	21	----	647	12	80	
		XXXV–22–6				513	15	73	919	15	80	
	-------	Wisc. All Seasons	------	------		258	1	83	287	1	85	
	-------	Commercial Glory	------	------		251	73	12	401	68	18	
IV	First	XXX–22–1	1921	1922	1923	250	14	79	726	16	75	Good type; preserved for further selection.
		XXX–22–2				249	16	79	549	15	82	
		XXX–22–3				253	10	85	241	14	79	
		XXX–22–4				248	18	78	462	11	83	
		XXX–22–5				254	14	80	342	11	75	Poor type; discarded.
		XXX–22–6				133	14	80	123	10	28	
	-------	Wisc. All Seasons	------	------		258	1	83	287	1	85	
	-------	Commercial Glory	------	------		251	73	12	401	68	18	

[a] The method used in numbering the cabbage strains is as follows: A Roman numeral was used to designate the original commercial variety from which the selection was made—XXX for Copenhagen Market and XXXV for Glory of Enkhuizen. The pair of Arabic figures next appearing—i. e., between the dashes (–20–, etc.)—indicate the year (1920, etc.) when the seed was grown, and the last figure is the number of the particular strain in question.

As to type, variation between strains is evident throughout. In Series I, strain XXXV–20–1, though showing a fair degree of resistance, was of inferior type and was therefore discarded. Although the other strain in the series, XXXV–20–4, was somewhat better, and further selection from it has been made, it is likely that it will eventually be discarded in favor of more satisfactory strains. Selections from the single strain of Series II are being continued for further study. The last two series, III and IV, offer the greatest promise (pl. 2). Of the six head strains in each, two from each series have been discarded because of deviation from the desired type. From the remaining strains, by rigid selection, several hundred typical heads have been preserved for further trials and for stock seed production.

SUMMARY

The progress with the selection of yellows-resistant second-early varieties of cabbage as here reported thus far confirms the writers' earlier belief that from any of the standard varieties of cabbage desirable resistant types may be obtained. While the work with the All Head Early and the Glory-Copenhagen types has not yet reached a finished state, the writers feel that they have advanced to the stage where the selections are approaching commercial value. They shall continue to make such improvements as are possible both as to type and as to resistance, and it is hoped that within a reasonable period these new strains will find their place in the regular commercial seed trade channels.

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THE COTTONY LEAK OF CUCUMBERS CAUSED BY PYTHIUM APHANIDERMATUM[1]

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INTRODUCTION

While several species of Pythium, notably *Pythium debaryanum* Hesse, have been found destructive to a wide variety of phanerogams in the seedling stage, and inimical to the best development of some of these hosts in later stages, the association of the genus with decay of commercial vegetable products, representing parts of plants approaching maturity, has not been frequently recorded. Perhaps the most generally known instance is represented by the "leak" of potato (*Solanum tuberosum* L.) tubers, apparently encountered by De Bary (*2*)[2] in Germany more than four decades ago, and more recently made the subject of special study in the United States by Hawkins (*8*). A soft rot of sweet pepper (*Capsicum annum* L., var. *grossum*) has been recorded by Lehman (*9*) from North Carolina as being due similarly to *Pythium debaryanum*, the decay always beginning at the blossom end, and affecting fruits not more than 6 or 8 inches from the ground. The same fungus is mentioned in the list of fungi thriving on fruit in Belgium by Él. and Ém. Marchal (*11*), who observed it on a pear (*Pyrus communis* L.) lying on damp ground.

MATERIAL EXAMINED

This paper deals with a disease of cucumber (*Cucumis sativus* L.) fruit which the writer first observed in specimens submitted to him June 8, 1922, by the food products inspector of the Bureau of Agricultural Economics at Washington, D. C., as being representative of a type of decay found responsible for considerable damage to a carlot shipped from St. George, S. C., June 2, 1922. Each fruit was entirely encased in a luxuriant cottony mycelial weft, matted down here and there as a wet membranous layer, at first sight thus suggesting being wrapped in absorbent cotton that had become moistened in places. The tissue in the interior was found very watery and of a peculiar texture, greatly softened, and so lacking in mechanical firmness as to be divided very readily with blunt instruments. Where not occupied by secondary bacterial invaders, the juices draining copiously from the incisions were only slightly turbid. The material gave off a peculiar odor rather inadequately described by the term "marshy"—not pleasant, but having little in common with the putrid smells characteristic of the decay of vegetables due to bacteria.

Since the original discovery of the trouble no additional material has been submitted to the writer, and from inquiry it would appear that the type of deterioration in question is not frequently encountered on the Washington market, or at least not in quantity. However, early in July, 1924, J. I. Lauritzen found several carload lots in both the Pittsburgh and the Buffalo markets, of which not inconsiderable portions were affected in exactly the manner described in the preceding paragraph. Almost simultaneously G. B. Ramsey observed the same decay with its characteristic display of cottony mycelium in a carload lot of cucumbers on the Chicago market, the shipment in this instance having originated in North Carolina. It is highly probable that in the case of the cucumbers grown in the Southeastern States the destruction from this trouble will generally be found greatest in the markets of our more remote northern cities, since, other things being equal, the quantity of cucumbers affected evidently increases with the length of time the shipment is in transit.

Microscopic examination of the specimens obtained on the Washington market revealed the fresh cottony growth as a mass of mycelium composed of nonseptate hyphae. Where the weft had been matted down as a wet membranous layer closely adhering to the substratum, innumerable thou-

[1] Received for publication, Aug. 20, 1924; issued August, 1925.

[2] Reference is made by number (italic) to "Literature cited," p. 1042.

sands of oogonia with antheridia and oospores, were found in all stages of development, the entire apparatus being readily recognizable as characteristic of the genus Pythium. The softened tissue was everywhere occupied by branching mycelium, the elements of which showed little evidence of definite orientation (fig. 1). At the points where the hyphae passed through the cell walls they were constricted to approximately half their normal diameter.

Pure cultures of the fungus were readily obtained by placing pieces of diseased tissue on corn-meal agar plates, and transferring portions of

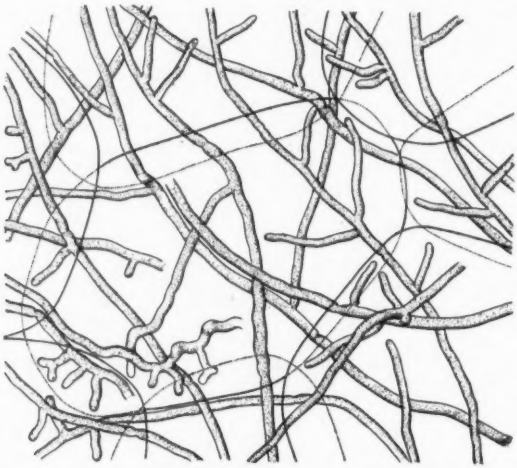


FIG. 1.—Section of cucumber affected with cottony leak, showing tissue occupied by abundance of branching hyphae, and constriction of latter where passing through host cell wall. × 250

mycelium from the margins of the resulting growth to tubes of sterile media. Through the courtesy of J. I. Lauritzen and G. B. Ramsey, transfers of the fungus isolated by them from the diseased material found in Pittsburgh and in Chicago, respectively, were also procured. In general appearance the cultures thus obtained were practically indistinguishable from cultures of the damping-off fungus, *Pythium debaryanum* Hesse. A minor but not insignificant difference could usually be made out in watching the development of the two types of parasites in parallel cultures, as under suitable conditions the cucumber fungus shows development of aerial mycelium in quantity by the end of the second day, whereas in cultures of the damping-off organism such development generally fails to ensue until the third day.

SOME MORPHOLOGICAL FEATURES

Zoosporangia of the fungus from cucumber fruits are readily obtained by putting pieces of invaded cucumber tissue (watermelon or squash tissue occupied by the parasite serve equally well), or thin slices from the surface of Lima-bean agar cultures, into a shallow layer of sterile water, which should preferably be renewed several times to wash away soluble staling products and excessive food materials. In the course of 2 to 5 hours an abundance of new structures are proliferated from the surface and periphery of the old mycelia, consisting of stout axial elements bearing swollen digitate and short diverticulate branches, these branches frequently undergoing close successive ramification to yield somewhat involved complexes corresponding to the structure discussed by Butler (*3*) as "budlike lateral processes." At other times the branches are fewer in number and at irregular intervals in open racemose arrangement. In any case, if the entire apparatus is well developed a number of septa varying from one or several to a dozen are inserted, thus bringing about the delimitation of a variable number of units, each of which may consist, for example, of a digitate branch with its secondary lobulate branches, or of a portion of the axial element with perhaps one or more diverticulate or branching laterals. After pronounced vacuolization of the protoplasm usual

for the sporangia of Pythium, and the development of an evacuation tube from the tip of one of the digitate elements, the contents of each unit escape to form a vesicle in which the zoospores are fashioned. The latter usually vary from 30 to 40 in number, but individual vesicles developing as few as half a dozen or as many as 60 are not rare. Under favorable conditions zoospore production is extraordinarily abundant, the amount of material that can conveniently be accommodated in a 10 cm. Petri dish giving rise to numbers estimated in excess of 100,000 in the course of an hour.

The organism evidently corresponds to a fungus apparently first noted in the literature as a variety of *Pythium gracile* Schenk by Butler (*3*), who in India found it parasitic on roots and base of stem of ginger (*Zingiber officinale* Rosc.) as well as on the roots of castor bean (*Ricinus communis* L.). Later, Subramaniam (*14*) investigated what he regarded as the same form more closely and set it off as a new species, *Pythium butleri*. In the meantime it had been encountered in the United States as the cause of a disease of radishes (*Raphanus sativus* L.) and sugar beets (*Beta vulgaris* L.) by Edson (*6*), who described it as *Rheosporangium aphanidermatum*, the type of a new genus of Saprolegniaceae. The similarity and apparent identity of the American and Indian forms were pointed out by Carpenter (*4*), who found the fungus associated especially with a destructive root rot of sugar cane (*Saccharum officinarum* L.) in Hawaii. More recently Fitzpatrick (*7*) made Carpenter's inferences effective in a nomenclatorial sense by combining Edson's specific name with both generic names, Pythium and Nematosporangium, the resulting binomials being presented as alternatives, choice between which was made dependent on the advisability of retaining or abandoning Schroeter's genus Nematosporangium as distinct from Pythium.

The genus Nematosporangium as defined by Schroeter (*13, p. 104*) was intended to include the forms having sporangia represented by filaments not differing from the vegetative hyphae, as contrasted with the forms possessing subspherical sporangia, which were to be retained in the genus Pythium. The distinction thus drawn is quite similar to that made by Butler (*3*), whose subgenera Aphragmium and Sphaerosporangium correspond closely to the genera recognized in the "Pflanzenfamilien." Recognition of the subspherical sporangium as a common characteristic of one group of forms is supported by excellent morphological evidence. However, the general view that the sporangia of the remaining forms consist of a simple or branching filament, analogous, for example, to the sporangium of Aphanomyces among the Saprolegniaceae, would appear to be in need of drastic revision. The sporangia characteristic of the parasite causing the cucumber decay discussed in this paper are represented, as has been pointed out, by units resulting from the septation of conspicuously swollen elements, corresponding to the structures which Ward (*15*) first figured and described in his account of a fungus he designated as *Pythium gracile* De Bary, and which later Butler discovered in all the members of the subgenus Aphragmium examined by him. Neither of these authors appears to have observed the participation of these structures in the formation of zoospores, Ward supposing them to serve as reservoirs of protoplasm for mycelial growth or the development of oogonia, while Butler assigned to them a probable capacity for surviving unfavorable conditions. In their studies of what presumably were forms identical with the one attacking cucumbers, Edson, Subramaniam, and Carpenter illustrated and discussed the same type of structures as "presporangia," "buds," and "sporangia," respectively, although perhaps without observing them in their most luxuriant development. It may be mentioned that even more distinctive development of this lobulate type of sporangium is exemplified in one of the two species with spiny oogonia found parasitic on watermelon fruits, the larger examples here being represented by a mulberrylike aggregation consisting frequently of more than a score of subglobose communicating elements, from which the contents are delivered through an evacuation tube into a vesicle giving rise to more than a hundred zoospores. The other spiny form (*5*) associated with decay of watermelons exhibits sporangia that may be regarded as a modification of the subspherical type, consisting generally of a subspherical part together with an adjacent part of one or both hyphal elements between which it is intercalated, the evacuation tube arising from the venterlike part, or from the filamentous part, or very frequently from near the juncture of the two. Because Schroeter's disposition makes no provision either for this transitional type of sporangium or for the distinctive lobulate type, his scheme to be usable

would seem to require modification either by appropriately amending the two genera recognized by him or including one or more additional genera. For the present, therefore, it seems best to retain the genus Pythium in its more inclusive sense, as employed in the writings of DeBary and Butler.

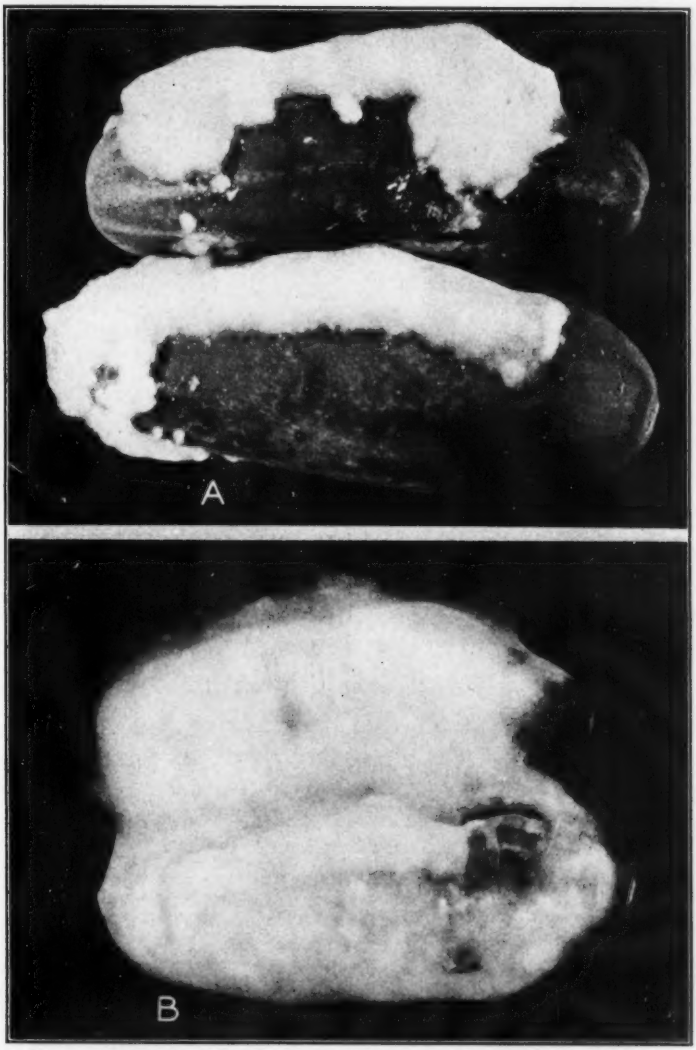
PATHOGENICITY

The pathogenicity of the three strains isolated from material obtained on the markets of Washington, Pittsburgh, and Chicago was repeatedly demonstrated by inoculation into healthy cucumber fruits. Pieces of mycelium from pure cultures were inserted into aseptic incisions, which then were sealed with sterile vaseline, and the cucumbers placed in glass chambers without additional water. Softening, involving the tissues usually for a radius of several centimeters, was manifest within 24 hours; in 48 hours the larger part of the cucumber was involved and aerial mycelium was present in quantity near the point of inoculation, while farther away it appeared in numerous small patches and minute white flecks that marked individual spots where the vigorous crowded hyphae had burst through the confining epidermis (pl. 1, A). At the end of the third day the whole fruit was frequently entirely clothed in cottony mycelium (pl. 1, B). That we are not dealing here with a specialized parasite became evident when altogether similar results were obtained by the use of strains morphologically identical with those derived from the cucumber but isolated from other sources: (1) From dead female nematodes, *Heterodera radicicola* (Greef.) Müller, in material supplied by N. A. Cobb and G. Steiner, where the occurrence of the fungus as a saprophyte or a possible parasite invading moribund specimens could not be clearly determined; (2) from pea (*Pisum sativum* L.) roots exhibiting symptoms of root-rot; and (3) from watermelon fruits affected with the buff blossom-end rot.

The cucumber parasite was tried out on a number of other economic cucurbitaceous fruits. As might be expected, watermelons were found highly susceptible to attack, the resulting decay being entirely similar to the buff blossom-end rot familiar to the writer as a field trouble apparently widely distributed in the Middle Atlantic States, and for the most part due to the identical fungus. Pattypan, vegetable marrow, and summer crookneck squashes, all representing varieties of *Cucurbita pepo* L., are as promptly attacked and destroyed as the cucumber and with the same luxuriant development of extramatrical mycelium (pl. 2, A, B). Experiments with muskmelons (*Cucumis melo* L.) have not been quite as satisfactory, owing to the difficulty of avoiding bacterial contamination, especially in riper specimens. In general, it appears that in the green condition in which this fruit is frequently found on the market, the muskmelon does not provide a substratum very suitable for the fungus, but that as maturity is approached the soft edible pulp is more readily invaded. It is possible that the fungus participates in the destruction of rejected muskmelons left in the field; a considerable portion of the abandoned muskmelons in some Delaware fields visited by the writer in 1922 exhibited, as the initial stage in decomposition, a very watery condition of the interior, associated with the peculiar marshy odor fairly presumptive of the presence of some species of Pythium.

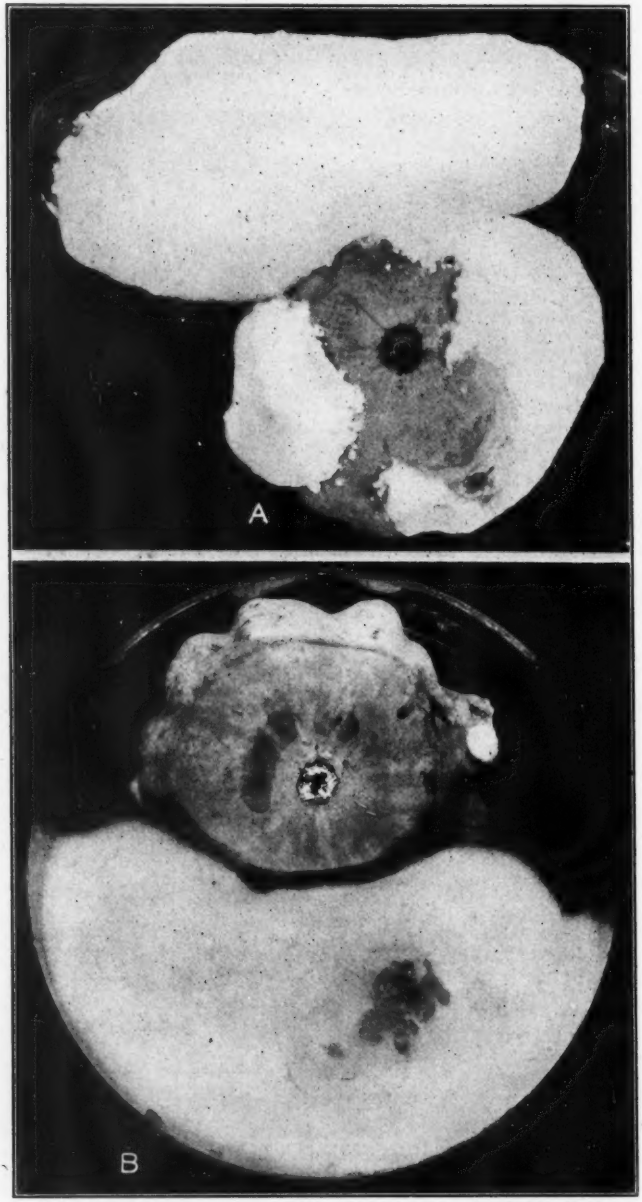
When inoculated under the rind of honeydew melons and cassaba melons (*Cucumis melo* L.), the fungus is able to establish itself, but subsequent development is markedly slow, sometimes being scarcely one-tenth as rapid as in cucumbers. The mycelium found in the tissues is of a compact, densely branching type, similar to that obtained on artificial media excessively rich in food materials, indicating that the juices of these fruits are too concentrated to permit of normal growth. Several inoculations into the flesh of Hubbard squash (*Cucurbita maxima* Duchesne) failed to result even in incipient infections, although the possibility that this vegetable is amenable to attack under other and more favorable conditions is not be to excluded.

While decay of cucumbers in transit has hitherto been found associated with only one species of Pythium, this is not because cucumbers are resistant to congeneric forms. In the course of routine procedure for obtaining the production of zoospores, for which purpose the tissue of cucurbitaceous fruits is not without merit, the writer has inoculated cucumbers with scores of strains having smooth oogonia, subspherical sporangia (or conidia), and fluffy aerial mycelium, belonging evidently to a number of related species—in short, with strains of the type traditionally and no doubt often correctly designated in papers on plant diseases as *Pythium debaryanum* Hesse. These strains have been isolated, for example, from the



A.—Two cucumbers 45 hours after inoculation with pure culture of strain of *Pythium aphanidermatum* isolated from diseased cucumber collected from carload lot at Washington, D. C., June, 1922. × ⅓

B.—Same two cucumbers as in A, but 24 hours later. × ⅓



A.—Vegetable marrow squash and pattypan squash 60 hours after inoculation at three points with pure culture of Washington strain of *Pythium aphanidermatum* isolated from diseased cucumber. × ½

B.—Three pattypan squashes 72 hours after inoculation with strain of *P. aphanidermatum* isolated from diseased cucumbers at Chicago, 1924. The profuse cottony mycelium in the lower part of figure has completely invested the two younger and more tender specimens. × ½

stems of cucumber plants affected with the trouble described by Atkinson (*1*) as canker; from diseased roots of herbaceous hosts, including garden peas, sweet peas (*Lathyrus odoratus* L.), rhubarb (*Rheum rhaponticum* L.), sweet potatoes (*Ipomoea batatas* Poir), cress (*Lepidium sativum* L.), and spinach (*Spinacea oleracea* L.); from roots of diseased seedlings of woody plants like *Pinus ponderosa* Dougl., *P. banksiana* Lamb., *P. sylvestris* L., *P. aristata* Engelm., and *Picea sitchensis* Trautv.; and from rose, pear, and geranium cuttings which had become diseased after being put in propagation beds. With relatively infrequent exceptions, the inoculated cucumber was attacked and the tissue invaded in much the same way as when *Pythium aphanidermatum* was employed, the rate of destruction for some forms being about equally rapid, while in the case of others advance was slower. All of the strains of Pythium isolated from separate lots of "leaky" potatoes and made available to the writer through the courtesy of G. K. K. Link have proved uniformly destructive, as have also about a dozen similar strains of the *P. debaryanum* type isolated from watermelons affected with a decay not readily distinguishable from the buff blossom end-rot due to *P. aphanidermatum*.

Although the several species of Pythium with subspherical sporangia (or conidia) and smooth oogonia show certain minor differences, in that some bring about greater softness in affected tissues, or a more watery condition than others, their effect in the interior of cucumber fruit is markedly similar to that produced by the parasite isolated from naturally infected material. The much more profuse development of aerial mycelium nevertheless provides a conspicuous characteristic by which attack by *Pythium aphanidermatum* can be distinguished from attack by the congeneric species that have been tried out. This feature appears sufficiently distinctive to merit attention in considering a common name for the disease under consideration. The term "cottony leak," descriptive of the most obvious symptoms of the malady, is proposed in this connection.

In its copious extramatrical development, moreover, is apparently to be found the characteristic to which *Pythium aphanidermatum* owes much of its destructiveness to cucumbers when packed as in commercial containers. The aerial mycelium of an individual fruit bearing an original infection grows out between adjacent fruits, partially or completely investing them. Laboratory experiments leave no room for doubt that such investment results in the infection of cucumbers, immediately if the epidermis is wounded, but without any considerable delay even if the epidermis is, as far as can be ascertained, altogether free of wounds. With the infection communicated from one fruit to another, each infected specimen gives rise in the course of 5 to 10 days to a "nest" of decaying cucumbers, including perhaps from a dozen to a score of individuals. Other species of Pythium with relatively feeble extramatrical development under conditions of only moderate humidity, such as generally prevail in produce cars, fail of passage from fruit to fruit, at least within reasonable periods of time. It is thus possible that if losses due to such species occur, the restriction of infection to single individuals might have occasioned their being overlooked by inspectors and others concerned in the examination and handling of food products.

In addition to cucumbers, the patty-pan squash, the summer crookneck squash, as well as the more delicate-skinned specimens of vegetable-marrow squash, have proved subject to infection by contact or investment with extramatrical mycelium of *Pythium aphanidermatum*. In cucurbitaceous fruits having a rind of indurated tissue like the watermelon, the cassaba, the honeydew melon, and the muskmelon, attempts at inoculation by means of surface contact have not given positive results.

It has been mentioned that some of the forms usually assigned to *Pythium debaryanum*, comprising, however, a relatively small minority, have failed to attack cucumbers when inoculated into incisions. A species not yet identified, provided with lobulate sporangia and hence closely related to but not identical with *P. aphanidermatum*, which was isolated from diseased corn roots, has shown no evidence of pathogenicity on cucumber fruit. The same statement holds true also of the two species with spiny oogonia (Artotrogus) responsible for the widespread chocolate blossom-end decay of watermelons, strains of these forms isolated from fruit thus affected as well as from pear cuttings, sweet-potato rootlets, and pea rootlets proving equally ineffective in producing decay of cucumbers. A third spiny species, in which the considerably larger oogonia are regularly borne on lateral branches, the swollen, somewhat contorted distal portion of which apparently serves as an intercalary antheridium, isolated only once from moribund rhubarb buds, similarly proved innocu-

ous to cucumbers. After securing negative results with three spiny forms, the writer was interested to discover that a fourth form derived from pea roots affected with the root-rot due to *Aphanomyces euteiches* Dr., and apparently different from the other three, attacked cucumbers with moderate vigor, the tissues becoming soft and watery.

In considering means of controlling losses from cottony leak, it is unfortunate that no information is available concerning the incidence of original infections. Knowledge as to whether such infections take place in the field or subsequent to picking would appear to be of primary importance. As the progress of the parasite at lower temperatures is relatively slow, and extramatrical development is reduced to small proportions in the absence of water of condensation and high humidity, attention to proper ventilation combined where practicable with refrigeration might be expected to check the spread of the infection to stock in good condition at the time it was packed.

The attention of students of plant diseases is directed to the very evident partiality of species of Pythium for the fruit of many Cucurbitaceae. Losses in the field due to their parasitism is undoubtedly more considerable than the paucity of references in the literature might lead one to suppose. Parisi's record (*12*) of the occurrence of *P. debaryanum* on the fruit of chayote (*Sechium edule* Sw.) in the botanical garden at Naples in December, 1920, is pertinent in this connection. Not less interesting is the very recent report by McRae (*10*) of the association of strains of Pythium with the decay of *Luffa acutangula* Roxb., *L. aegyptiaca* Mill., *Trichosanthes anguina* L., and *Lagenaria vulgaris* Ser. in India, where these members of the Cucurbitaceae are grown as vegetables.

SUMMARY

Cucumbers grown in the Southeastern States have, on arrival at the northern markets, shown occasional losses due to a disease for which the term "cottony leak" is proposed. It is caused by a species of Pythium identified as *Pythium aphanidermatum* (Eds.) Fitz., the infection being communicated from diseased fruits to adjacent healthy ones by copious production of extramatrical mycelium.

The fungus is strongly parasitic on watermelons, on which host it is responsible for one of the blossom-end rots widely prevalent in the Middle Atlantic States. On inoculation it is rapidly destructive to patty-pan, vegetable-marrow, and summer crookneck squashes.

The sorting out of cucumbers harboring the fungus and the lowering of humidity and temperature by adequate ventilation, combined possibly with refrigeration, are indicated as means for controlling the trouble.

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COMPARATIVE STUDIES OF PYTHIUM DEBARYANUM AND TWO RELATED SPECIES FROM GERANIUM[1]

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INTRODUCTION

Stem rots of geranium cuttings (Pelargonium spp.) have been frequently reported in the literature and ascribed to various microorganisms. Ward (*20*)[2] cultured *Pythium debaryanum* on live Pelargonium cuttings in the course of his classic studies with this fungus. Prillieux and Delacroix (*18*) described *Bacillus caulivorus* as the causal agent of a stem "gangrene" of Pelargonium, potato, clematis, and begonia, and reported *B. pyocyanus* on Pelargonium from Germany. Galloway (*12*) noted a stem discoloration, accompanied by shrivelling and softening, which extended upward from the severed end until the whole stem was involved. Many bacteria but no fungi were observed filling the cells of the advancing area of discoloration. The disease was considered possibly identical with that of Prillieux and Delacroix, which was also later described by Chifflot in a résumé of geranium diseases (*9*). This writer also described a Pelargonium stem rot due to Botrytis sp. Peters (*17*) obtained *P. debaryanum* from diseased geranium stems, which are well illustrated in a colored plate showing typical progressive blackening of the cuttings. He made successful pure culture inoculations and also reproduced the disease by placing healthy cuttings in soil infested with this organism. Inoculation usually resulted in early death; infected cuttings seldom remained partially diseased. Johnson (*16*) isolated this organism from blackened geranium cuttings. Buddin and Wakefield (*5*) obtained *P. debaryanum*, as well as *Botrytis cinerea*, on geranium stems.

The writer has had four species of Pythium under observation since 1919, isolated from diseased geranium cuttings. One of these, *Pythium complectens*, n. sp., was described in a previous paper (*4*). The second (labeled *B* throughout this study) corresponds morphologically to *P. debaryanum* as described by Hesse (*15*), De Bary (*1, 2, 3*), Ward (*20*), Butler (*6, 7*), and others who have worked with and defined the morphological characters of this fungus. The remaining two, which have also proved pathogenic in pure culture inoculation experiments, differ morphologically and physiologically from *P. debaryanum* but are clearly related to it. The present paper is a report of a comparative study of organism *B* and the two related fungi, which have not been found to be wholly identical with any previously described Pythium species.

THE DISEASE

SIGNS

The symptoms of disease caused by any of the Pythium species here described consist of a progressive blackening, shrivelling, and necrosis, starting at the base of the cutting and rapidly involving the entire stem and the petioles (pl. 1). The leaves wilt down when the petioles are reached and death of the entire plant soon ensues. The pith is hollowed out by a soft, wet rot. Epidermal cylinders (except in very young and succulent cuttings) and fibrovascular bundles are not attacked except in the late stages, when secondary organisms enter into consideration. Little difference in the character of the lesions caused by any of these fungi can be observed except in the rate of progress, which is similar for *B*[3] (*P. debaryanum*) and *A*, but distinctly less rapid for *D*. The complete destruction of the cutting is in marked contrast with the stoppage of infection previously described for *P.*

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[2] Reference is made by number (italic) to "Literature cited," 1062.

[3] For the sake of brevity the isolations were lettered *A* to *D* in their order of isolation, and will be so designated in this paper as far as the section in which their taxonomy is considered; *B* referring to *P. debaryanum*, *C* to *P. complectens*, *A* to the large conidial Pythium, and *D* to the form producing the characteristically irregular, swollen, asexual fruiting bodies.

complectens, where a cork layer laid down in advance of infection prevents further progress of the hyphae after nfection has already extended some distance from the point of inoculation. The rate of progress of infection is lways less rapid where comparatively mature plants are involved (pl. 2), and may be localized when the epidermal cylinder is thickly cutinized and the basal tissues are old and woody.

The hyaline, coenocytic hyphae of these fungi may be observed in and between cells of the less discolored advancing area, particularly as long strands along the fibrovascular system (pl. 3, A). Farther back the fruiting bodies are formed, including oospores and conidia in the case of *B* (*P. debaryanum*); conidia only were formed in tissues by the other two Pythium spp. Bacteria were frequently observed in the more decayed tissues, particularly in xylem cells, but not in the less infected regions where advancing hyphae could be seen.

ISOLATION

P. debaryanum (*B*) and the large conidia form *A* were first isolated, occurring together in a plate colony made from a single diseased geranium from the Washington greenhouses. They were separated by making single-spore cultures from conidia, those of *A* being by far the larger and readily recognizable. Form *D* was obtained alone in a later isolation. Repeated isolations from naturally blackened and diseased geranium cuttings in the Department of Agriculture greenhouses have yielded these fungi, occurring sometimes together, usually singly. The methods of isolation used have been described in the paper on *P. complectens* (*4*). Cultural studies from single-spore isolations soon showed that these fungi are not identical, nor corresponding to previously described species of Pythium with the exception of *B*, the *P. debaryanum* isolation.

PATHOGENICITY

Controlled inoculation experiments involving some 230 cuttings in 17 inoculation series since isolation have shown that the disease can be reproduced with great uniformity when the inoculum is placed at the cut base of fresh Pelargonium cuttings in sterilized soil, using any of the three isolations. Progressive discoloration and rot occurred as in naturally infected cuttings from the severed end up; check plants formed a callus as a rule and rooted normally. No differences in the symptoms produced could be observed with either isolation, except in the rate of progress; *Pythium debaryanum* (*B*) and isolation *A* were the most severe. Death ensued within 6 to 10 days, depending on the organism used. Material fixed in Flemming's strong solution and in Merckel's fluid and sectioned showed the hyphae within the tissues, conidia in the case of *A*, conidia and oospores in the case of *B*. Each was readily reisolated from advancing margins of the discoloration. Repeated reisolations with subsequent inoculation have shown their ability to attack geranium cuttings. Cross-inoculations on coleus, begonia, cucumber seedlings, and radish seedlings result in soft rots in the first two hosts and typical damping off in the seedlings, form *B* causing by far the most severe infection. *A* and *D* required a longer incubation period in the case of the seedlings and caused slower progress of the disease. In one experiment where cuttings were placed in soil which had previously contained plants artificially infected with Pythium species, four out of five were infected where *B* had been used, two were killed and three showed basal blackening when *A* had been used, and four out of five showed infection when *D* had been used, indicating the rôle of the soil as a carrier. After four or more years in culture, there is a distinct reduction of virulence evident in a slower progress of discoloration and lower percentages of infection compared with the uniformly complete infections obtained early in the work.

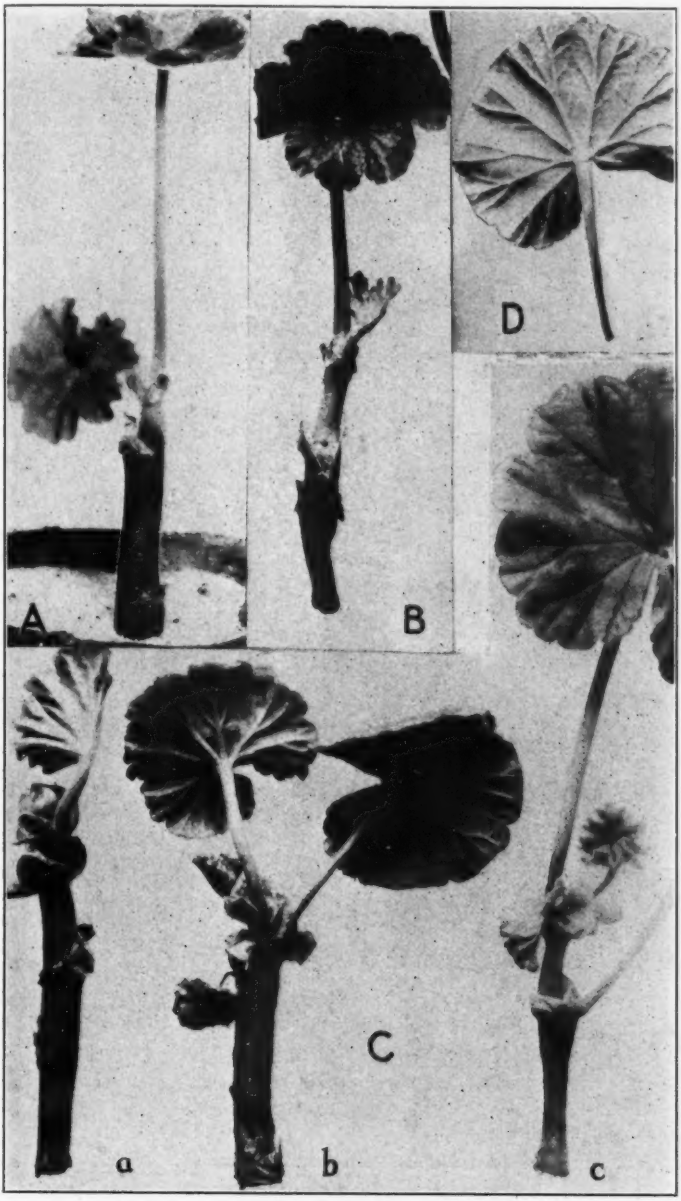
The comparative rates of discoloration caused by each of the organisms are shown below in data from one of the inoculation experiments (September 15, 1921):

ISOLATION A.—Ten plants inoculated at the base. Discoloration averaged 35.9 mm. up the stem by the second day; 59.4 mm. by the fifth day, with five plants collapsed. Eight were dead the sixth day, and the discoloration on the remainder averaged 67.2 mm.

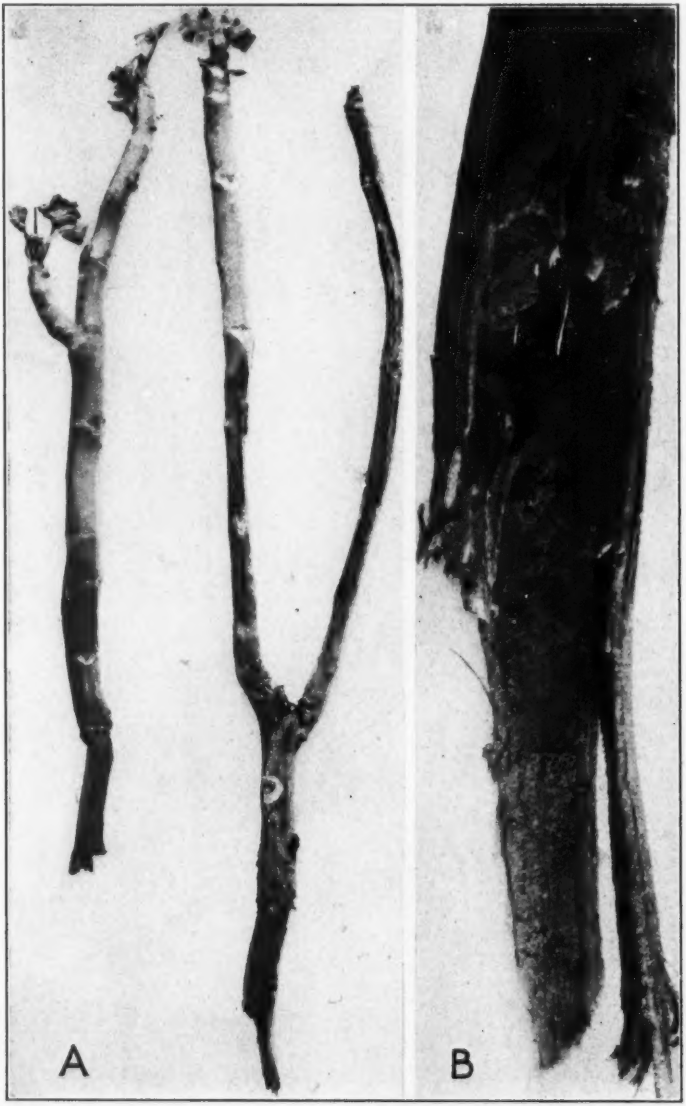
ISOLATION B.—Ten plants. Discoloration reached an average of 32.6 mm. up the stem by the second day; eight had collapsed by the fifth day, the remainder averaging 63.7 mm. All were dead and on the ground the sixth day.

ISOLATION D.—Ten plants. Discoloration reached an average of 21.6 mm. the second day, 32.7 the fifth day, 38.5 the sixth day. None were dead till the tenth day. All had collapsed four days later.

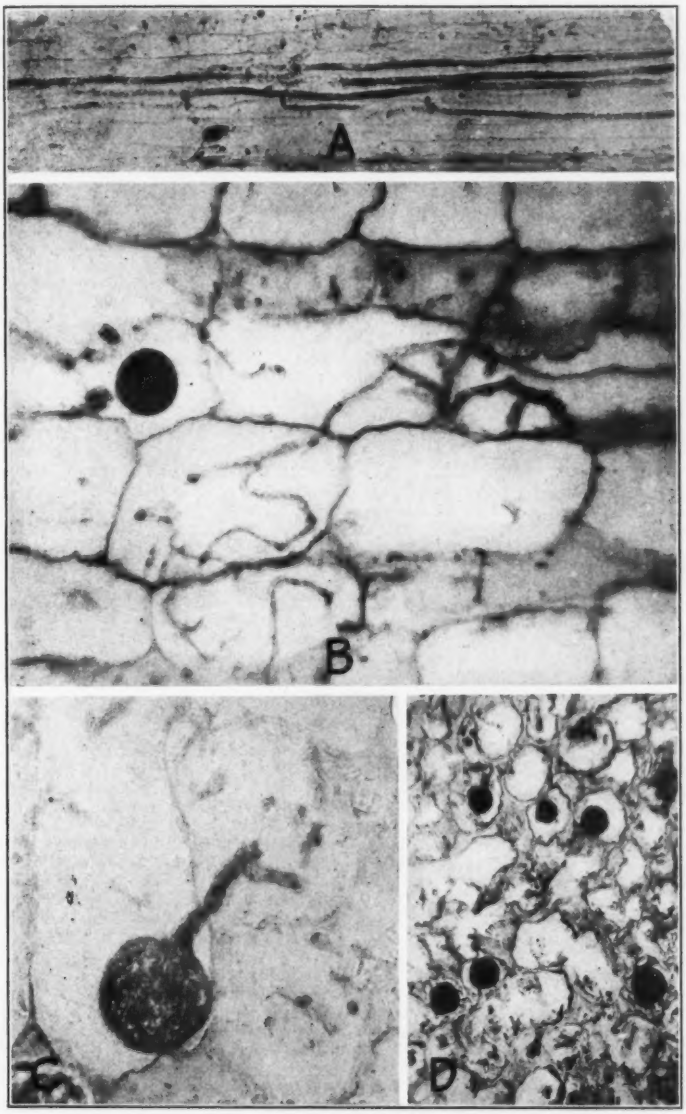
Ten checks remained healthy, formed a callus and rooted long before infected plants began to collapse.



A.—Naturally infected geranium cutting; *P. debaryanum* was isolated
B.—Cutting naturally infected with *P. debaryanum* var. *Pelargonii*, Washington greenhouses
C.—Artificial inoculations, fifth day; Ca, *P. debaryanum;* Cb, *P. splendens;* Cc, *P. debaryanum* var. *Pelargonii*
D.—Leaf from Cb, showing the shriveling and discoloration of the base of the petiole



A.—Mature plants from Enid, Okla., from which *P. complectens* was isolated (1923)
B.—Lower part of stem right, enlarged nearly five times. The rotting away of pith, leaving the epidermal cylinder intact for some time, was characteristic of each of the organisms studied



A.—Mycelium of *P. splendens*, running between companion cells in long strands
B.—Mycelium of same, in pith cells; also conidium
C.—Conidium being formed in pith cell. Note constriction of hyphae through cell wall
D.—Conidia sprinkled through the pith

PATHOLOGICAL HISTOLOGY

The hyphae are both intercellular and intracellular, and may be observed in all tissues except the fibrovascular long before the cells collapse. Constriction at passage through the cell wall is the rule (pl. 3, C). Long strands run between the companion cells, branching out at intervals into the pith and cortex. Here the development of the mycelium is profuse, often forming coiled nests within cells and branching abundantly and irregularly. The host protoplasm is rapidly disorganized; but nuclei and starch grains are still recognizable even in late stages of tissue disintegration.

The large conidia of *A* are formed abundantly within the cells, sometimes in the intercellular spaces. In the latter case and when formed in the elongated companion cells or xylem they may be flattened out or compressed in accordance with the shape of the surrounding host cell walls. Two or three conidia may be found in a large pith cell. Oospores of *A* have not been observed within the tissues; *P. debaryanum* (*B*), however, forms them in abundance, as well as conidia, though to a lesser extent. No oospores of *D* were found within infected tissues. This organism forms round conidia to a small extent; nests of hyphae, irregularly swollen places in the mycelium and profuse branching were more frequently observed. The curious sickle-shaped bodies so abundantly formed in cultures of all three were not found in the tissues.

Discoloration of the host cell walls by oxidation products of the disorganized cell contents is followed by collapse and soft rot accelerated by the action of secondary organisms on the dead cells. The stems of succulent cuttings are rapidly reduced to a black flaccid mass which remains in the soil if the still healthy part is pulled off, and acts as a source of infection.

THE FUNGI

MORPHOLOGY

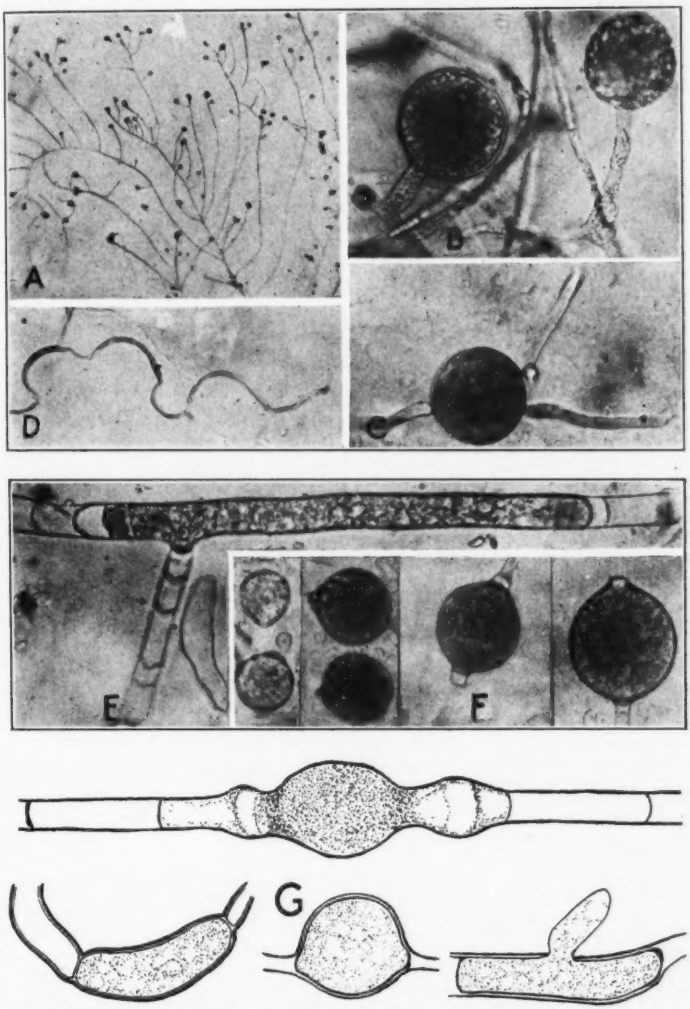
The morphology of *Pythium debaryanum* as it occurred in the writer's cultures will be briefly described, for comparison with the related fungi herein discussed. The hyphae are 3.5 μ to 10.0 μ thick, average 6.4 μ, richly branching from strongly developed main hyphae. The small subsidiary branches curve in all directions, resulting in plate colonies which appear uniform and finely granular to the unaided eye; this type of growth is in sharp contrast with the combed-silk effect characteristic of *P. complectens*, caused by parallel radial growth of the branches. Variations from the normal hyphae are to be found in irregular knotted masses or coils, and in clavate, sickle-shaped bodies abundantly developed within two days of growth on plates (pl. 4, D). Carpenter (*8*) figures similar bodies in *Pythium butleri* from sugar cane (his pl. 16, figs. 1 and 2). In the writer's cultures they were developed at the interface of agar and glass, and near solid particles in the media, indicating a possible appressorial nature. Chains of these clavate bodies, which bore a striking resemblance to antheridia except that they were larger, and not near oogonia, were found in plate cultures of each of the Pythium species under observation.

Conidia are smooth-walled, subspherical, terminal, or intercalary, 16.6 μ to 26.2 μ in diameter, averaging 21.7 μ. Germination takes place by germ tubes, usually one. Zoospore formation has not been observed.

Swollen intercalary bodies are sometimes found in old cultures where the media is drying down. These appear more irregular in size and shape than the conidia formed in the early stage of growth, but also germinate by pushing out a germ tube.

Oospores are found in great abundance on corn meal agar and oatmeal agar and are far more frequent than conidia. The oogonia are 16.8 μ to 25.8 μ in diameter, averaging 25.1 μ; oospores are 14.7 μ to 21.3 μ in diameter, averaging 18.1 μ. The oospores lie free in the oogonia. Both are smooth-walled. Antheridia are clavate, single, less frequently two or three per oogonium; a well-marked fertilization tube is put forth from the tip of the antheridium which is applied to the oogonium wall. Fertilization has been frequently followed through in living material and does not differ essentially from the accounts of De Bary and Ward, except in the inception of the exospore wall, which takes place by the tangential extension of a peripheral disk as described for *P. complectens* (*4*). Germination of the oospores has not been observed.

The fourth Pythium (*D*) resembles the above organism in the size of the hyphae and in the method of branching. Round, smooth conidia are produced in moderation but show greater variation in size, ranging from 12.8 μ to 27.7 μ, average 20.1 μ. The most characteristic feature is the intercalary for-



A.—*Pythium splendens*, conidial formation terminally at ends of short branches. ×12+
B.—Swelling up of tips of conidiophores to form conidia. ×500 circa
C.—Germination of conidia (several germ tubes) in tap water
D.—Sickle-shaped, clavate bodies formed in chains on plates; present in all the forms studied. ×50
E.—Retraction of protoplasm to form the large intercalary body, showing septa successively laid down
F.—Round conidia, *P. debaryanum* var. *Pelargonii*. ×550
G.—Irregular, swollen intercalary bodies characteristic of this organism, also showing germination

mation in plate cultures, within seven days after inoculation, of irregular swollen bodies filled with a dense protoplasm which has withdrawn from adjacent regions of the hyphae, laying down septa as it contracts (pl. 4, E). Such a condition is a not uncommon phenomenon in a variety of old fungus cultures; in this case, however, it is produced quite normally after a few days of growth. The general contraction of the protoplasm into these bodies with abundant septation of the empty hyphae occurs in 7 to 10 days after inoculation of the plates. Such colonies are granular but otherwise almost transparent and without the filamentous structure usually visible to the eye in fungus cultures. Hand-lens inspection reveals a multitude of short straight crystal-like bodies, which are the septa formed in the clear hyphae by the retracting protoplasm. Germination of these resting bodies takes place by a tube, as in the case of the round conidia.

A second characteristic of *D* is the scarcity of oospores, contrasting sharply with the profusion of oospores produced by *B* on plates of nearly all media. None were obtained for 14 months after the original isolation, though 16 media were tried. They finally appeared in hanging drops of sterile oatmeal decoction four days after inoculation, and have since appeared sporadically in cornmeal agar plates. The conditions necessary for oospore formation are not known, aside from the facts that long-continued growth and transfers on artificial media preceded their appearance, and that they are most likely to appear immediately around and on the mycelium used as the inoculum, rather than on the fresh growth.

In measurements the oospores of *D* vary little from those of *B*, ranging from 15.9 μ to 19.9 μ, averaging 17.8 μ. One to four antheridia are present, all emptying their contents. They are usually broader at the apex than are antheridia of *B*, and differ also in that they often lie appressed to the oogonium along their entire length. Contraction of the oosphere and fertilization through a tube occurs as described in this group. Complete maturation is however the exception rather than the rule; the contracted fertilized oosphere often degenerates into a mass of oily globules which later merge into a large vacuole filling the oogonium except for a peripheral layer of hyaline granules, no oospore wall being formed. Oospores that have come to maturity lie free in the oogonium and are smooth walled. The walls are distinctly thinner than those of *B* (pl. 5, C), and are hyaline or yellowish. The contents are granular except for a single eccentric vacuole.

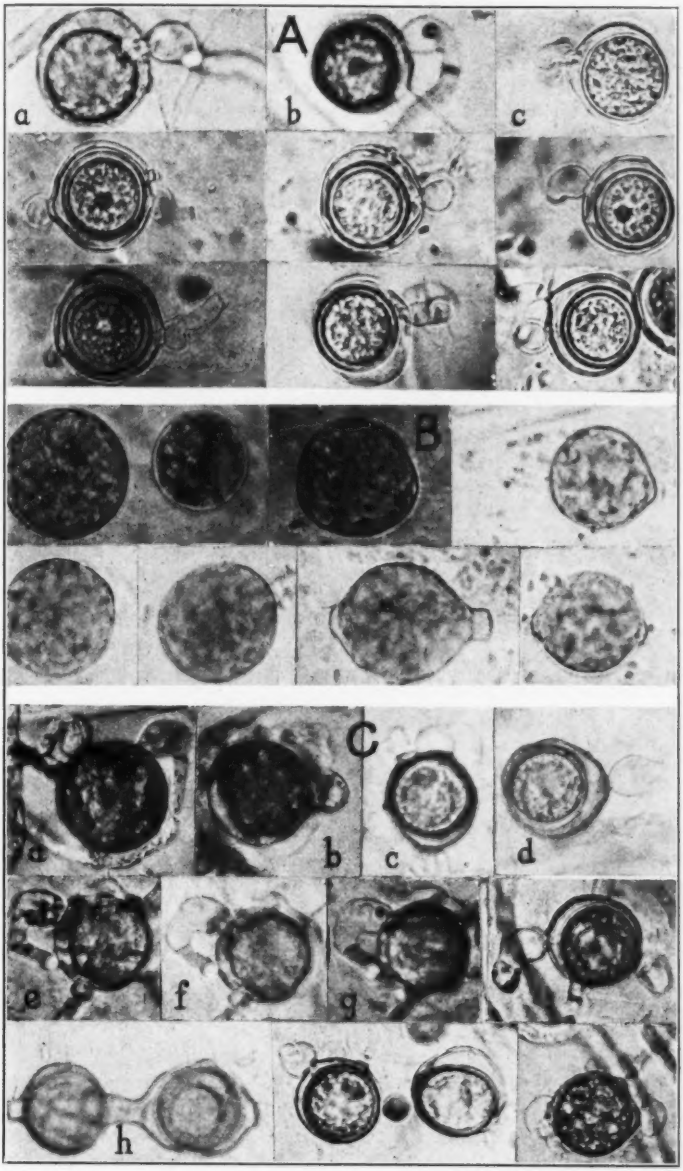
Attempts at germinating the oospores of *D*, including the use of freezing, alternate temperatures, etherization, and soaking in water, have not succeeded. The round conidia and the swollen irregular bodies are clearly the stages on which the organism is dependent for dissemination and the tiding over of unfavorable conditions, since oospores have not been found in nature and are so scarce in culture.

The sickle-shaped bodies characteristic of these Pythium spp. were developed in plate cultures two days after inoculation.

Type *A*, the organism first isolated, is characterized morphologically (1) by the abundant formation of spherical terminal conidia on all media and in the host plant, much larger than those of *B* (21.7 μ to 48.9 μ, average 36.2 μ); (2) by a comparatively small production of large oogonia (25.5 μ to 34.7 μ, average 31.7 μ) and oospores (21.3 μ to 29.8 μ, average 26.6 μ) accompanied regularly by three to eight antheridia. Comparative measurements from this organism and *B* are shown in Figures 1 and 2. Hyphae are 3.5 μ to 9.2 μ wide, average 6.4 μ, and consist of thick main branches with curving lateral branches arising at acute and right angles, constricted at the point of origin. The sickle-shaped bodies are also present, often growing in chains (pl. 4, D).

The conidia appear within two days on culture media, and are formed by the swelling up of a hyphal tip. Intercalary conidia have not been observed, in marked contrast with the abundance of this type in cultures of the other organisms studied. The conidia are smooth and thin walled, and are filled with a densely granular protoplasm which becomes vacuolate with age. Conidia from potato cylinders, beef agar, and potato agar without dextrose are abnormally hyaline and collapse sooner than those from media rich in sugars and readily available food, as sugar-beet agar and oatmeal agar. Drying out of the media in all cases is followed or accompanied by collapse and death of the conidia. Those in the depth of the media, therefore less exposed to drying, are more likely to remain plump and viable, cultures sometimes remaining viable after 10 months.

The conidia of *A* are formed in such abundance on all media that the colonies rapidly assume a finely granu-



A.—Type *B. Pythium debaryanum*, oospores in various stages of fertilization and maturation. ×750
B.—*P. debaryanum*, conidia. ×750
C.—*P. debaryanum* var. *Pelargonii*, oospores. ×750. Fertilization and maturation. Successive stages in fertilization of a single oogone in e-f-g. Note intercalary oogonia, plurality of antheridia, and broad apex of antheridia; also the thin wall of the oospore

lar appearance, and individual conidia may be observed with a low-power hand-lens along the edges of the growth when it has reached the glass sides. Frequently each lateral branch of a hypha becomes a conidiophore off by a septum and drops off. Persistent conidia and germination *in situ* are exceptional. Zoospore formation has not been observed, even when the same environmental conditions are applied which induced their formation

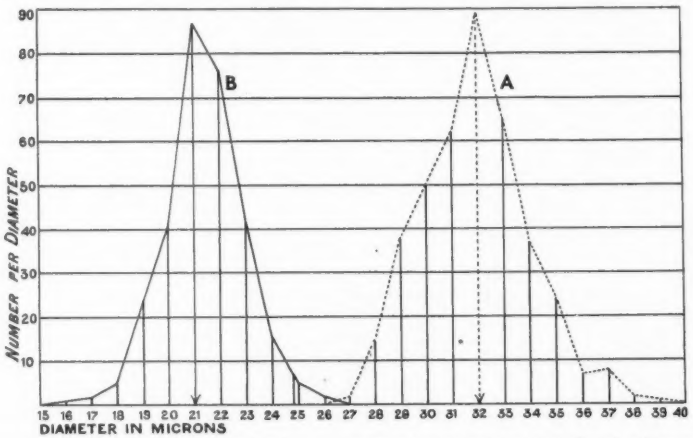


FIG. 1.—Measurements of oogonia of *P. debaryanum* (300) and of *P. splendens* (400) plotted as frequency curve

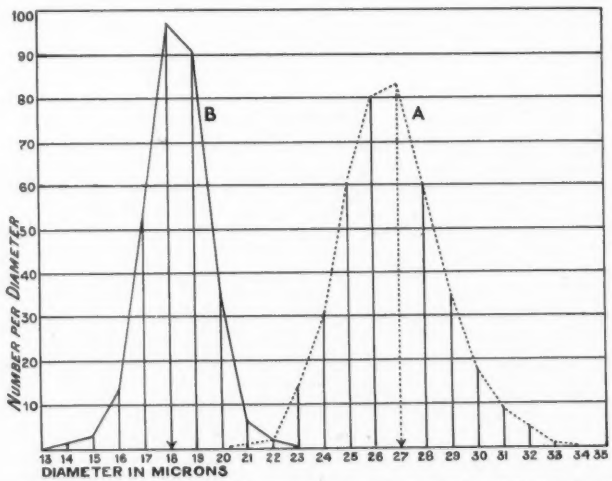


FIG. 2.—Measurements of oospores of *P. debaryanum* (300) and of *P. splendens* (400) plotted as frequency curve

(pl. 4, A). The most prolific appearance of these bodies was observed in colonies held at 30° C., which is also the optimum temperature for mass growth.

Germination in *A* may take place immediately after the conidium is cut in *Pythium complectens*. When placed in distilled or tap water, in potato juice, prune juice, and oatmeal decoction, from two to six tubes are put forth from each conidia, the number being larger in the richer substrata. The latter also induce more rapid and

abundant germination. Each germ tube becomes a "main" hypha and can be traced as such for a considerable distance; short side branches are given off profusely, with occasional longer lateral branches which soon acquire the greater thickness and length characteristic of the "main" hyphae.

Terminal microconidia, scarcely larger than the hyphal width, are sometimes found. The size of the normal conidia varies with the substratum, but is always much larger than that of *P. debaryanum* or *D* from the same medium. Culturing over a period of four years has not markedly affected the size of the conidia, although the oospores have become noticeably reduced in size.

OOSPORES OF A.—Cultures of the original isolations were grown on various media for nearly two years before oospores were obtained. The first were found on a bit of old mycelium which had been used as inoculum for a plate of Knopf's synthetic agar, on which the organism makes a scanty, spreading growth. Subcultures of this, and inocula from two-months-old oatmeal agar cultures which had been kept in the icebox at least a month, subsequently yielded oospores quite regularly on Knopf's agar, later on cornmeal and carrot agars. The oospores appeared at first on and immediately around the inoculum; in later cultures they were produced in the general body of the medium, synchronously with the conidia. Oospores could usually be found in aggregates on distinct hyphal groups which could be traced some distance, indicating oospore production to be a function of special hyphae.

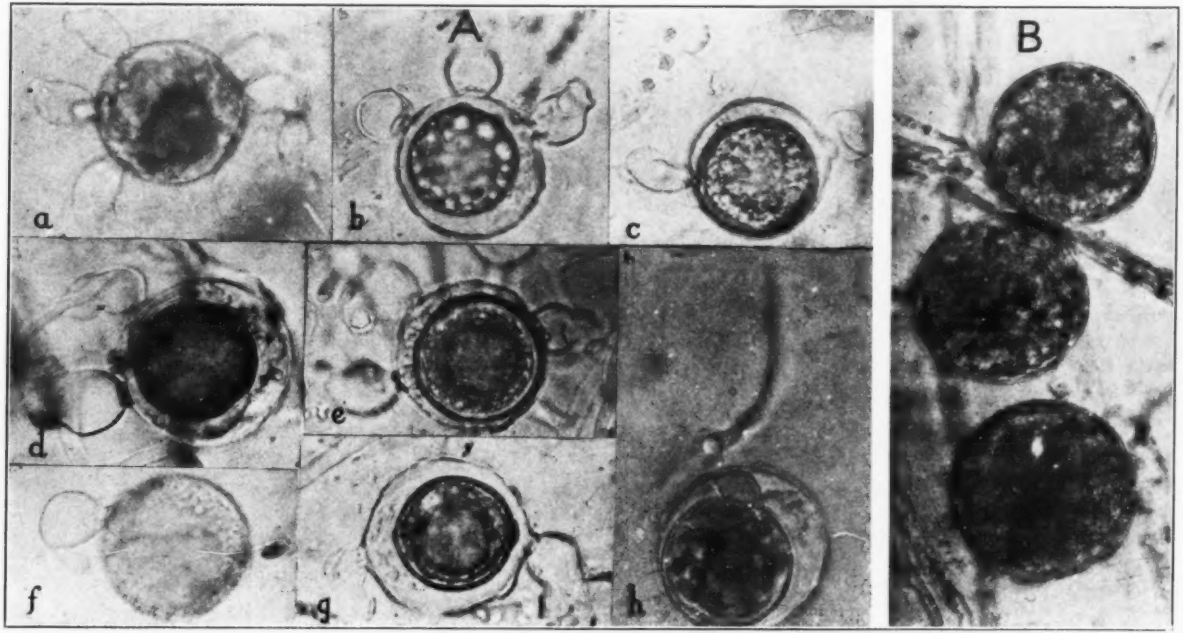
Heterothallism is, however, not indicated, since the cultures were descendants of single spore cultures which are readily made on account of the large size of the conidia. The factors responsible for sexual reproduction as contrasted with conidial reproduction are not clear-cut, since inoculations of a batch of plates occasionally resulted in purely conidial formation in some of the plates. Inoculations on cornmeal agar from old, chilled oatmeal agar cultures could generally be counted upon to produce oospores, though always in moderation.

The spherical oogonia of *A* are smaller than the conidia and contain a more finely granular, nonvacuolate hyaline protoplasm. They are soon enlaced by adjacent antheridia, which may arise below the oogonium or, more usually, from neighboring hyphae. They are clavate, much larger than those of *B* (compare pls. 6 and 5, which were photographed at the same enlargement), and from three to eight are found regularly with each oogonium. Each is fused at its apex with the oogonial wall and sends a fertilization tube across to the contracted oosphere. At maturity, all antheridia around the oospore are found empty. All do not, however, empty directly into the oosphere; observations on living material indicated that a membrane is formed after the emptying of one or possibly two antheridia into the oosphere, effectively preventing fertilization by the remainder. This is shown in Plate 6, A, *g*, where the contents of the left-hand antheridium have been extruded into the space between original wall and oosphere. The latter has evidently been fertilized by the antheridium at the right and formed a membrane before the others could empty into it, the membrane subsequently thickening into the oospore wall. Similar cases may be seen in Plate 6, A, *b* and *e*.

In one instance observed during fertilization a single antheridium of *A* had already emptied into the oosphere, which was rounded up and surrounded by a very thin membrane. A second antheridium was seen to extrude its contents through the fertilization tube which touched the oosphere membrane, the contents spreading out, however, over the oosphere surface and quickly retracting into the antheridium, where they degenerated into oily globules. Occasionally abortion takes place, such as was observed in *D*. The contracted oosphere fails to form a definite wall, turns into a mass of large, bright oily globules (pl. 6, fig. A, *b*), which expand and fill the oogonium (pl. 6, fig. A, *a*), later fusing into a single large vacuole nearly filling the oogonium except for a surrounding layer of granular, hyaline cytoplasm (pl. 6, A, *f*).

More frequently fertilization is followed by thickening of the oospore walls, accompanied by changes in the oospore contents, which result in the final appearance of a large excentric vacuole surrounded by a densely granular but hyaline cytoplasm. Both oogonial and oospore walls remain smooth and hyaline; the mature oospore lies free in the oogonium but occupies a space proportionally less than in the case of *B*. The ratio of oospore to oogonium in the former is 1 : 1.2, in the latter 1 : 1.1.

Germination of a few oospores of *A* was obtained by pouring aerated tap water over a month-old cornmeal agar plate culture containing oospores (pl.



A.—*Pythium splendens*, oospores. ×750. Note the numerous antheridia, the size compared with the oospores on Plate 5 (same magnification); germination shown in *h*

B.—Conidia of same. × 750. Compare with Plate 5, same magnification

6, A, *h*). The endospore wall is dissolved, and a single thick tube breaks the exospore and oogonial walls. The contents of the oospore gradually pass into the tube, which continues to grow and form a mycelium. Zoospore formation has not been observed.

CULTURAL STUDIES

The cultural characters of these fungi were studied along with those of *Pythium complectens*, on 16 media in 4 culture series. The terminology suggested by Harsch and Long (*13*) and also followed recently by Fritz (*11*) has been followed in describing the character of growth. These studies have shown specific differences which have remained constant since original isolation. Except on four media, the four fungi were readily distinguishable from each other macroscopically. Cultures of each organism were always made in triplicate tubes on each medium. Some of the more prominent diagnostic characters are as follows:

On oatmeal agar and on sugar-beet agar the growth of *A* plugged the tube up to the top of the slant, forming a narrow, compact web across the bore. This persisted when the rest of the mycelium below it had matted down. No such web was formed by the other fungi (pl. 7, A and E.)

The growth of *D* on most media was sharply characterized by being much more compact and appressed to the slant than that of *A* or *B*. This may be seen in the side views of the tubes in plates.

No aerial growth was produced by *A* on cornmeal agar, carrot agar, potato agar, potato dextrose agar, and potato cylinders (slight aerial on the last after four weeks), contrasting sharply with the abundant aerial growth of the other two fungi (pl. 8.)

A characteristic feature of *A* was the granular appearance of all cultures due to the abundant production of large conidia.

Growth of *B* on potato cylinders was distinctive, due to the abundance of loose, fluffy aerial mycelium. That of *A* was entirely prostrate, that of *D* was felty, compact and closely appressed to the cylinder.

The media used throughout was prepared uniformly in accordance with the formulas of the Laboratory of Plant Pathology. Directions as given by Smith (*19*) were followed in the case of nutrient beef-broth agar, potato cylinders, sugar-beet cylinders, and bean pods. The formulas for the remainder were taken from the files of the laboratory and are appended.

CORNMEAL AGAR

To 4 teaspoonfuls of corn meal add 1 liter of distilled water. Keep in water bath for 1 hour, temperature about 50° C. Filter through cotton. Add 1¼ per cent agar flour to the filtrate. Steam 1 hour, filter through cotton, tube, and sterilize in the autoclave for 15 minutes at 115° C.

OATMEAL AGAR

50 gm. oatmeal in 500 c. c. H_2O. Steam in bath; strain through gauze; add 2 per cent agar flour (mixed in cold water); make up to 500 c. c.; steam, tube, and autoclave 15 minutes at 115° C.

CARROT, SUGAR-BEET, STRING-BEAN AGARS

Wash thoroughly, weigh and add water to double the weight of solid material. Let simmer. Strain and add 1½ per cent agar flour; steam three-quarters of an hour, filter, tube, autoclave or steam. For geranium agar, use twenty times as much water, 3 per cent agar, and steam.

POTATO AGAR (STRONG INFUSION, OXIDIZED)

500 gm. potato, 1,000 c. c. distilled H_2O, 1½ per cent agar flour; weigh potatoes, put through meat grinder, add water, and let stand 1 hour. Strain through gauze to remove cellulose. Make up to volume. Steam juice to clarify, and filter through cotton. Add agar, steam three-quarters of an hour. Filter through cotton, tube, and autoclave for 15 minutes at 115° C.

Potato dextrose agar: Add 10 per cent dextrose.

CONGO-RED AGAR

To 1,000 c. c. distilled H_2O add 10 gm. saccharose (Mercks); 1 gm. K_2HPO_4 (dipotassium phosphate); 0.20 gm. $MgSO_4$ (magnesium sulphate); 15 gm. agar flour (powdered); 0.10 gm. congo-red (powdered Grubler's). Steam water and all salts for one-half hour, then add the congo-red. Filter through cotton and tube. Tube, autoclave for 15 minutes at 115° C.

MILK RICE (SOYKA)

(1) Measure out 50 c. c. nutrient bouillon and 150 c. c. milk and mix thoroughly. (2) Weigh out 100 gm. rice powder and rub it up in a mortar with the milk and broth mixture. (3) Fill the paste into sterile tubes. (4) Sterilize in the steamer at 100° C. for 30 minutes on each of 3 consecutive days. (A pure white opaque medium is thus formed.)

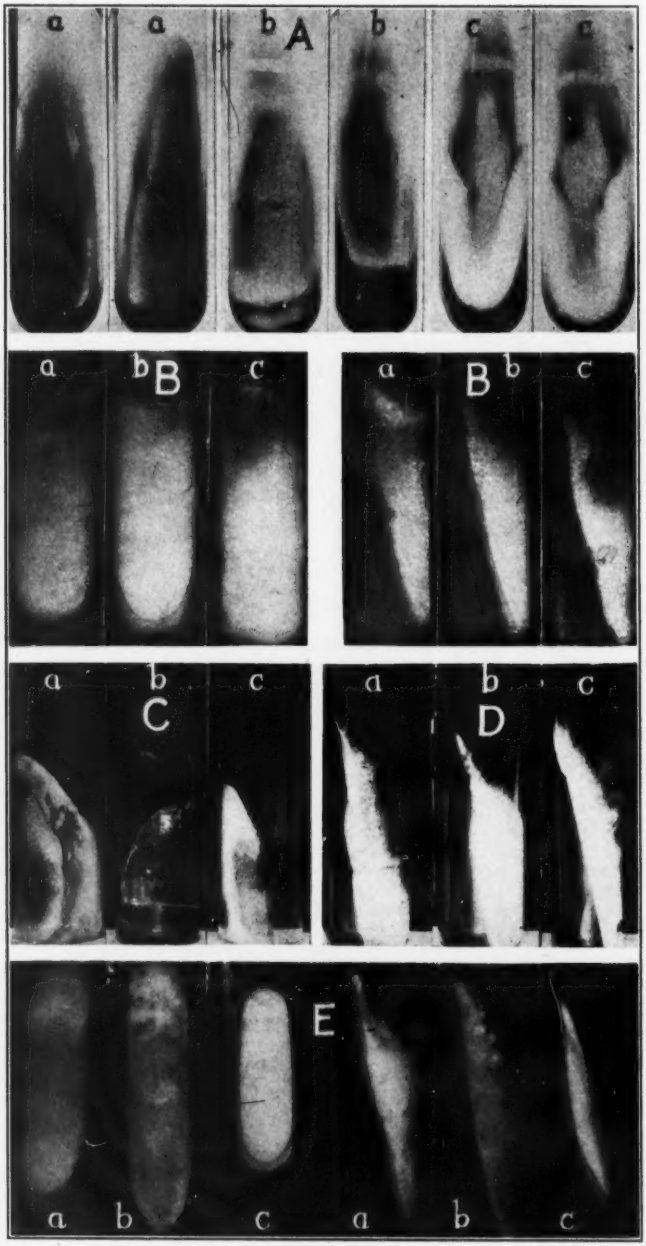
CORNMEAL FLASKS (FOR THE CULTIVATION OF FUNGI)

Into a 100 c. c. Erlenmeyer flask put a heaping teaspoonful of cornmeal. Put in enough distilled H_2O to thoroughly wet and with a little surplus. Stir round to mix, plug, and autoclave for 25 minutes at 120° C.

OATMEAL AGAR.—*A*. Abundant cobwebby white mycelium plugging tube up to top of slant; characterized by the formation of a compact web across the bore of the tube at the top of the slant, persisting after the growth below has matted down (three weeks). Vague outline at base.

B. Differs from *A* in the absence of a covering web, in the more compact mycelium, and in the sharp outline of the growth at the base of the slant against the glass.

D. More compact than *B*, white growth, plugging tube only halfway up slant; sharp outline at base.



A.—Growth on Congo Red agar; *a, a, Pythium splendens; b, b, P. debaryanum; c, c, P. debaryanum* var. *Pelargonii*
B.—Oatmeal agar; *a, a, P. splendens; b, b, P. debaryanum* var. *Pelargonii*. Front and side views
C.—Bean agar. Same lettering as in B
D.—Bean agar. Same lettering as in B
E.—Sugar-beet agar. Same lettering as in B

Pythium debaryanum and Related Species from Geranium

Plate 8

A.—Carrot agar

B.—Potato dextrose agar

SUGAR-BEET AGAR.—*A*. Growth similar to that on oatmeal agar, except that the mat at the base of the slant against the glass is thicker and sharply outlined; web present.

B. As in oatmeal agar, except for the indefinite outline at base.

D. As in oatmeal agar cultures, but more compact and appressed to slant, white at base, becoming deep olive buff at the tip where there is a persistent felty appressed mass.

BEAN AGAR.—*A*. First week's growth prostrate, forming a smooth thick mat, finely granular on account of the abundant large conidia; aerial growth during second week, cobwebby hyphae plugging lower part of slant up to third of slant, the rest more closely appressed, forming an open dry film; flattens down during third week to a sodden prostrate mat, except for a few small dry patches of aerial mycelium on the upper part of the slant.

B. Abundant aerial growth during the first week, plugging tube up to two-thirds of the way up the slant, more compact and felty at top of slant; drying down after three weeks to form an appressed thin film.

D. Aerial growth during first week, much more compact than *B*, flattening down to a thin dry film after three weeks.

POTATO CYLINDERS.—*A*. Prostrate, sodden wet mat over lower part of cylinder, scanty growth at top. Short downy white aerial growth after four weeks, matting down again in three months.

B. Abundant white aerial growth plugging part of the tube above slant within a week; becoming more compact in three weeks, entirely matted down in three months to a sodden glistening mass, with cobwebby strands from cylinder to glass.

D. Thick, white, closely appressed aerial growth within a week, more compact than *B*, not plugging tube, matting down in three months to a dry mat, dull. Smoke-gray to light grayish olive.

SOYKA RICE SLANT.—*A*. Compact, felty white growth, closely appressed to slant, later flattening down to a dry white film.

B. Abundant fluffy white growth plugging tube up to two-thirds of slant, flattening down after two weeks to a sodden mat.

D. Closely appressed aerial growth, more compact than *A*, forming a dry white film.

BEAN PODS.—*A*. Cobwebby film of mycelium covering pod and reaching to the glass, flattening down after two months to a sodden wet mat.

B. Tubes plugged up to top of pod with thick white mass of hyphae during first week; this mats down within 11 days to form a thick wet mat over the surface of the pod and water, leaving a few cobwebby strands bearing drops of exudate.

D. Early growth aerial, cottony, more compact than *B*, not plugging tube, remains aerial longer than *B*; mats down after three weeks.

SUGAR-BEET CYLINDERS.—*A*. Growth prostrate during first week, later aerial cobwebby to cottony in lower part, downy appressed at top; after three weeks flattening down to a sodden mat.

B. Abundant aerial growth from the start, plugging the tube up to top of slant with a thick weft of cottony white mycelium which flattens down after three weeks to a wrinkled wet mat with occasional hyphae between cylinder and glass.

D. Similar to *B*.

CARROT AGAR.—*A*. Growth prostrate, finely granular (due to conidia), smoke gray; small compact white tufts at top of slant; thin wefts of cobwebby aerial mycelium at edges of slant.

B. Abundant fluffy white growth, plugging tube four-fifths of the way up the slant; compact felty mass at tip; flattening down after three weeks, from base of slant upward to form a prostrate hyaline wet mat.

D. Differs from *B* in the very compact, appressed white aerial growth, not plugging tube; felty, closely textured at top, becoming cottony at the base; flattening down after a month to a thick dry mat.

POTATO DEXTROSE AGAR.—*A*. Similar to growth on carrot agar, except for the color, which is pale olive buff to light grayish olive; more pronounced aerial growth at edges of slant reaching to the glass.

B. Similar to growth on carrot agar.

D. Similar to growth on carrot agar, except that matting down takes place earlier in *D* than in *B* (two to three weeks), beginning at center and leaving cobwebby mycelium at the base and a smooth, closely appressed dry film at the tip.

POTATO AGAR, NO DEXTROSE.—*A*. Thick, prostrate, wet mat, uniformly granular, smoke gray to grayish olive, with slight felted aerial growth at upper half appearing after three weeks.

B. Cobwebby white aerial growth appearing during first four days, matting down within a week to form a prostrate gelatinous film, thickened at the base of the slant, pale smoke-gray to light grayish olive, aerial growth

again within three weeks, cottony at base, felted and compact at tip, matting down within three months.

D. The aerial growth is loose and more closely appressed to the slant.

CORNMEAL AGAR TUBES.—*A.* Thin, prostrate hyaline mat, thicker toward base of slant, finely granular due to abundant conidia. No aerial growth, except a dried felty layer at the tip.

B. Cobwebby white mycelium plugging tube up to half of slant, merging into a thin prostrate weft in the upper half; entire aerial mass flattens down to a gelatinous mat within two weeks.

D. Aerial growth less abundant than *B*, completely matting in 10 days.

CONGO-RED AGAR.—*A.* Scanty surface growth, except over lower half of slant, surface dry, shiny, abundant subsurface growth reaching throughout the agar, uniformly granular, conidia formed in abundance along the glass at the edge of the slant; prostrate except for cobwebby wefts at edges of slant appearing after two weeks. No color change after three months.

B. Abundant white surface growth, becoming aerial within a week, loose, cobwebby; plugging tube three-fourths up-slant; quickly matting down (two weeks) to a thin dry layer of closely appressed hyphae, aerial mycelium around edges persisting; abundant uniform subsurface growth of more compact texture than *A*. No color change after three months.

D. Differs from *B* in earlier and more abundant aerial growth, which is also much more compact and white and slower in matting down. No color change after three months. Note: Tubes of *P. complectens* showed a color change to Indian purple.

VIABILITY

Duplicate tube cultures of each organism on various media, which had been kept at room temperature (18° C. in winter to 35° C. in summer) were tested for viability as described for *Pythium complectens*. Melted cornmeal agar at 38° was poured over the slants after absorption of sterile oatmeal decoction; transfers from cultures which showed growth were compared with stock cultures and were also identified microscopically. The results are summarized below.

Isolation B.—Dead after 11½ months on potato agar, potato dextrose agar, Soyka rice, beef agar, geranium agar, and in one tube of oatmeal agar; also after 7 and 8 months on potato agar and Congo-red agar. Alive after 11½ months on cornmeal agar, bean agar, and in one tube of oatmeal agar; also after 5½ months on potato dextrose agar.

Isolation D.—Dead on all media kept longer than 5½ months.

Isolation A.—Dead on all media kept longer than 5½ months, except on carrot agar where it was recovered after 9 months.

The high viability of *B* as contrasted with that of the other two fungi, should be compared with the equally high viability of *Pythium complectens*, which was recovered after 11½ months on carrot agar and bean agar. There can be little doubt that the relative viability of these species of Pythium is correlated with the production of oospores, which is abundant in *P. debaryanum* and *P. complectens* and relatively scarce in the other two, as was pointed out in the description of their morphology.

TEMPERATURE RELATIONS

The accompanying chart (fig. 3) outlines the growth curves averaged from two experiments with plates in ice thermostats and warm incubators, ranging from 3° C. to 35.5°. Triplicate plates of cornmeal agar of each organism were placed in each compartment and measurements of the colony diameter were made at 24-hour intervals. Inoculations were made from a three-days old cornmeal agar plate culture which was cut up into one-sixteenth inch squares, each square then being planted in the center of the fresh plate. Before inoculation all plates were kept overnight in their respective compartments to avoid lag effects.

The behavior of these fungi at the lower temperatures presents some interesting features.

Isolation *D* shows the lowest minimum, the colonies growing appreciably at 6° C. within 24 hours, and reaching a diameter of 41 mm. in 144 hours (not shown on chart). Growth was evident at 3° within 48 hours, and, when placed directly on ice, showed a slow growth at 96 hours, a characteristic separating it immediately from the remaining Pythium species studied. In fact, the quickest way of differentiating this organism from the others was to place freshly inoculated plates in the lowest-temperature compartments; the plate showing the most growth, or in fact any growth at all at or near 6°, within 24 hours, could be counted on as being isolation *D*.

Colonies of isolation *B* showed growth at 6° only after 72 hours, reach-

ing 7 mm. at 144 hours; no growth was observed at 3°.

Isolation *A* showed the highest minimum, showing no growth at 6° even after 144 hours and at 11° only after 72 hours.

The optimum temperatures of the three forms do not differ greatly, best growth taking place between 27° and 30°. Between 20° and 35.5°, however, the growth of *A* constantly outstripped that of the other two fungi. It was also characterized by a higher maximum.

The temperature experiments indicate distinct physiological differences between these fungi, which are particularly evident and constant in the ability to grow at low temperatures, and in the greater luxuriance of growth of *A* within the range of temperatures at which cultures are usually incubated.

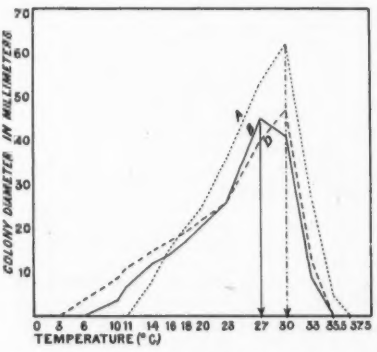


FIG. 3.—Temperature relations plotted in colony diameter growth for 25 hours

TAXONOMY

The morphological character of these fungi places them in Butler's group of Pythium species which includes forms with a smooth-walled oospore lying free in a smooth-walled oogonium, and with spherical conidia or sporangia. These include (1) *P. debaryanum*, (2) *P. vexans*, (3) *P. ultimum*, (4) *P. anguillulae aceti*. The first is considered identical with the writer's isolation *B* in measurements, relative abundance of oospores and conidia, in cultural characters so far as detailed by Hawkins (*14*) and by Edson (*10*), and in appearance as figured by De Bary, Ward, and others. Zoospores were not obtained, but neither were they found by Ward, Edson, or Johnson (*16*). It also corresponds with *P. debaryanum* as figured from geranium by Peters (*17*), although the originality of his drawings is not clear in view of the fact that he repeated Hesse's mistake of placing a single cilium on the zoospores, the biciliate nature of which was pointed out by De Bary (*3*).

Isolation *D*, while corresponding closely to *P. debaryanum* in measurements, differs in the following respects: (1) Constant and readily distinguishable cultural differences; (2) specific temperature relations, evident by growth at the lowest temperature of the four species of Pythium studied; (3) a distinctly slower infection rate as compared with *B* and *A;* (4) a preponderant tendency toward a sexual reproduction, oospores appearing only rarely and then often aborted; (5) a thinner oospore wall; (6) greater variation in the size of conidia as compared with *B;* (7) the appearance, within a short time after inoculating plates, of irregular swollen bodies formed by the retraction of protoplasm with the laying down of successive septa, germinating by a germ tube and also differing in size and absence of lobing from the "presporangia" of *P. butleri*.

In the above respects *D* does not correspond with any of the other species grouped with but distinguished from *Pythium debaryanum*. In its parasitism and scarcity of oospores it differs from *P. ultimum; P. intermedium*, in which oospores are unknown, is characterized by catenulate conidia, which are not present in this fungus. The writer considers it a variety of *P. debaryanum*, to which it is clearly closely related, and proposes the name *Pythium debaryanum* var. *pelargonii*. The technical description follows:

Pythium debaryanum var. **pelargonii** nov. var.

Hyphae coenocytic, hyaline, richly branching from thick main hyphae, 3.8 μ to 9.8 μ wide, average 6.2 μ; oospores spherical or subspherical, smooth, diameter 15.9 μ to 19.9 μ, average 17.8 μ; free in the smooth-walled oogonium, thin-walled, scarce in culture media, often aborted; oogonial diameter 17.4 μ to 21.9 μ, average 20.1 μ; one to four antheridia, clavate, often adhering to the oogonium along their entire length, usually arising from a neighboring branch; conidia spherical or subspherical, terminal and intercalary, smooth, diameter 12.8 μ to 27.7 μ, average 20.1 μ; hyaline, germinating by one to three tubes, formed abundantly on media; sickle-shaped bodies formed singly or in chains two days after inoculations of plates; irregular swollen intercalary bodies formed in plates within seven days after inoculation, by

retraction of protoplasm with laving down of successive septa, germinating by germ tube; minimum temperature 6° C. at 24 hours, lower than *Pythium debaryanum*, from which it is further distinguishable culturally, particularly in a more compact habit of growth. Parasitic on Pelargonium sp., causing a stem rot.

In the case of *A*, the smooth oospore lying free in the smooth oogonium (specific according to Butler) separates it immediately from other large-conidial and multi-antheridial species. Conidia are unknown in *Pythium proliferum*, whose zoosporangia are large, spherical, and proliferating, with oospores not filling the oogonium. *P. megalacanthum* is multi-antheridial, but the oogonial walls are sculptured.

Type *A* differs from *Pythium debaryanum* and the allied species both morphologically and physiologically, in the following respects: (1) The constant larger size of the fruiting bodies compared with those of the other fungi studied on the same media; (2) constant and recognizable cultural differences; (3) preponderance of conidial production; (4) specific temperature relations, expressed in a higher minimum, and in more luxuriant growth than the others at 20° to 35.5° C.; (5) difference in the size ratio of oospore to oogonium; (6) constant accompaniment of the oogonium by more than one antheridium, ranging from three to eight under conditions identical with those at which *P. debaryanum* produced one or rarely more than two; it differs from *P. ultimum* in parasitism, measurements and absence of intercalary conidia, and from *P. intermedium* in the absence of catenulate conidia. It is considered a distinct species, for which the name *Pythium splendens*, n. sp., is proposed. The technical description is appended.

Pythium splendens, n. sp.:

Hyphae 3.5 to 9.2 μ wide, average 6.4 μ; oospores spherical to ellipsoid, smooth walled, lying free in the smooth oogonium; ratio oospore to oogonium 1:1.2; oospores thick walled, produced sporadically in cultures; three to eight antheridia, clavate, arising at the oogonial stalk and from neighboring branches; oospores germinating by germ tube within a month of formation; conidia spherical, always terminal, smooth walled, large, 21.7 μ to 48.9 μ in diameter, average 36.2 μ; hyaline, darker on rich media, germinating by two to six germ tubes; sickle-shaped, clavate bodies formed singly and in chains on plate media two days after inoculation; temperature ranges 10° to 37.5° C., optimum 30°; minimum higher than that of *P. debaryanum* and more luxuriant growth between 20° and 35.5; readily distinguishable by specific cultural characters. Parasitic on Pelargonium, in the tissues of which conidia are abundantly formed.

SUMMARY

Stem rots of Pelargonium cuttings caused by *Pythium debaryanum*, *P. debaryanum* var. *Pelargonii*, nov. var., and *P. splendens*, n. sp., are described and the comparative morphology and physiology of these organisms is detailed.

The signs of the disease consist of a blackening and shriveling, starting at the cut base and ultimately involving the entire plant in a soft rot. *P. debaryanum* var. *Pelargonii* differs, so far as infection is concerned, only in the slower progress of the discoloration.

Inoculation experiments with single-spore cultures and subsequent reisolations have demonstrated the pathogenicity of these organisms on Pelargonium, coleus, begonia, cucumber seedlings, and radish seedlings, *P. debaryanum* proving the most pathogenic on the last two.

Cultural characters on 16 media are described. The three fungi are readily distinguishable macroscopically.

Pythium debaryanum var. *Pelargonii* is characterized by the lowest minimum temperature, a character sufficiently constant and specific to identify it experimentally within 24 hours. *P. splendens* shows the most luxuriant growth of the three at 20° to 35.5° C.

Pythium debaryanum shows the highest viability on media and was readily recovered after 11½ months at room temperature. The other two were dead after 5½ months, except *P. splendens*, which was recovered in one case after 8 months. The correlation between oospore production and viability is pointed out.

Pythium debaryanum var. *Pelargonii* is characterized morphologically by greater size variation of conidia and their preponderance over oospores, which are produced only rarely and are often aborted; its oospores are thin-walled; one to four antheridia are present; irregular swollen intercalary bodies are formed through retraction of the protoplasm, which lays down successive septa; these resting bodies are not related to aging of the media but are produced within seven days of plate inoculation.

Pythium splendens is characterized morphologically by larger conidia, oospores, and oogonia; by the constant presence of three to eight antheridia; by the terminal formation of conidia, no intercalary ones being found; by the preponderance of conidia, oospores being formed only sporadically; by germination of conidia with two to six germ tubes.

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VARIATION IN THE KHERSON OAT AT AKRON, COLORADO[1]

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INTRODUCTION

Few oat varieties grown in the United States surpass the Kherson in economic importance or in potential value. It is one of the most widely distributed early varieties, especially in the Corn Belt and the central section of the Great Plains area. The extensive distribution of Kherson and Sixty-Day oats in the United States in 1919 is shown by the map (fig. 1) prepared from statistics obtained in an oat varietal survey conducted by the Office of Cereal Investigations in cooperation with the then Bureau of Crop Estimates. Among the 10 leading varieties in 1919, Kherson and Sixty-Day ranked fourth in acreage. When the acreages of important selections such as Albion (Iowa No. 103), Iowar, Gopher, Richland (Iowa No. 105), and States Pride (Wisconsin No. 7) are added to those of the original variety, this type of oat easily ranks third in importance in the United States, being exceeded only by Silvermine and Red Rustproof.

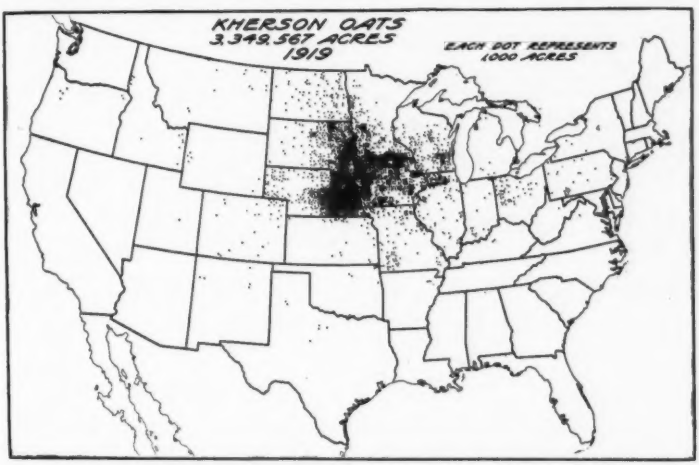

FIG. 1.—Outline map of the United States, showing the distribution of Kherson (Sixty-Day) oat in 1919

REVIEW OF LITERATURE

Carleton (*2*, *3*)[3], Lyon (*15*), Warburton (*24*), and Warburton and Stanton (*26*) have presented historical accounts of the introduction of the Kherson and Sixty-Day into the United States. All of the foregoing writers, and also Etheridge (*5*), have classified Kherson as belonging to *Avena sativa* and have published general or botanical descriptions of the variety. Warburton and Stanton (*26*) state that "botanically the Kherson and Sixty-Day oats can not be distinguished one from the other, * * * the varieties are

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[3] Reference is made by number (italic) to "Literature cited," p. 1081.

identical and the names, therefore, are synonymous * * *." They are so considered in this paper.

Norton (*18*) points out that most oat varieties probably consist of numerous strains. The work of Coffman, Parker, and Quisenberry (*4*) shows this to be especially true of the Burt variety, which was found to consist of numerous distinct types, some of which differ widely. Warburton and Stanton (*26*) have stated that both white-kerneled and yellow-kerneled selections have been made from Kherson or Sixty-Day. Stanton (*19*) and many others have made reports on experiments conducted with selections from this variety. Reports by Love (*10, 11, 12*), Williams and Welton (*28*), Warburton, Burnett, and Love (*25*), Surface and Zinn (*21*), Welton and Gearhart (*27*), Kiesselbach and Ratcliff (*8*), Burnett (*1*), Hayes and Garber (*7*), Leith and Delwiche (*9*), and Burnett, Stanton, and Warburton[1] have described selections made from Kherson or Sixty-Day.

Panicles and spikelets of important selections from Kherson or Sixty-Day are shown in Plate 1.

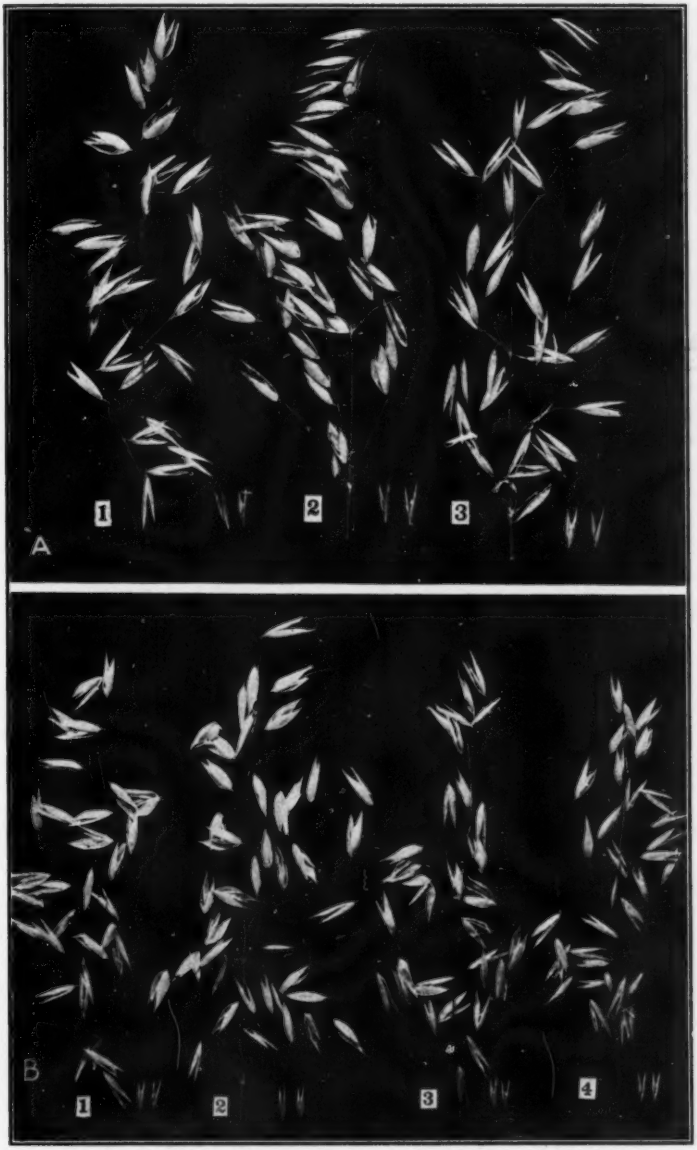
Many investigators have used strains of Kherson or Sixty-Day as parental material in oat hybridization, both with the object of producing improved economic varieties and for genetic studies. A correct knowledge of the variety itself is therefore of considerable importance.

Surface (*20*) made one of the first reports on a cross in which the Kherson oat was studied genetically. He crossed this variety on *Avena fatua*, the common wild oat. He states that the pure-line selection of Kherson used in this cross had been grown for five years and had always bred true for all characters. According to him the awn was seldom present in this strain of Kherson. When present it was found only on the lower kernel and then was very weak. The kernels of this selection had no basal scar and seldom had basal hairs, although spikelets having lower kernels with one or two long hairs on the side of the callus occasionally were found. He further states that all cultivated varieties of oats which have come to his notice may have this slight pubescence at the base of the lower grain and that some varieties have it more marked than others. Surface also found the F_1 of his cross to be intermediate between the two parents in nearly all respects. In F_2 he observed that the basal scar segregated into a ratio of one prominent, two intermediate, and one absent. He observed linkage between basal scar and the presence of hairs on the base. The absence of basal scar was found to be apparently dominant, or at least partially so, over the "wild" type of base having a very pronounced scar. No marked relation was noted between the yellow color of the Kherson strain he used and absence of awns. He attributed the fact that F_2 awnless plants failed to breed true in F_3 either to the presence of additional genes or to the explanation of Nilsson-Ehle (*17*) that external conditions may greatly affect the production of awns in cultivated oats. Surface further states: "General observations also indicate that the character of awning varies widely even within a pure line, and it may happen that plants which are genetically awned will, because of environmental or other conditions, show no awns." He found evidence of linkage between cultivated base form and absence of hairs and also between yellow color and absence of basal scar.

Love and Fraser (*13*) crossed awnless Sixty-Day with Burt and with Red Rustproof (Red Texas), both of which bore awns of the "weak" type. The F_1 of both crosses was almost awnless. They observed that awnless F_2 plants did not always produce progeny all of which were awnless in F_3, a fact which they attribute to environmental factors preventing or obscuring the production of awns in the F_2 generation. They believe the "strong" awn type to be recessive, but the awnless condition could not be considered as being entirely dominant. Apparently the explanation of Nilsson-Ehle (*17*), which assumes that yellow color in oats is linked with an inhibitory factor for awn production, is favored. It is suggested by Love and Fraser that probably the results obtained by Surface (*20*) in crossing Kherson oats with the wild *Avena fatua* may be similarly explained—i. e., Kherson may carry a factor inhibitory to awning.

Love and Craig (*14*) report results obtained in crossing *Avena fatua* × *Avena sativa* variety Sixty-Day. Their results, however, do not agree with those of Surface. They point out that in view of the possibility of obtaining different strains from a variety, particularly so far as the inheritance is concerned, as shown by yield, etc., it is not surprising that these results should not agree. Love and Craig conclude that the Sixty-Day strain they used

[1] BURNETT, L. C., STANTON, T. R., and WARBURTON, C. W. IMPROVED OAT VARIETIES FOR THE CORN BELT U. S. Dept. Agr. Bul. 1343. 1925. (In press.)



Panicles and spikelets of Kherson and some yellow and white kerneled selections

A. (1) Kherson; (2) Richland (Iowa No. 105); and (3) States Pride (Wisconsin No. 7)
B. (1) Albion (Iowa No. 103); (2) Iowar; (3) Nebraska No. 21; and (4) Cole

carries an inhibitor for awning which is linked with yellow color, and state that the third generation tends to substantiate the conclusions drawn from the study of the second generation. They also observed in F_2 and F_3 correlation between yellow color and the absence of basal scar as well as between yellow color and absence of basal hairs.

Fraser (*6*) discusses the results obtained in the study of crosses, Sixty-Day × Burt and Sixty-Day × Early Ripe (Burt). He believes that the Sixty-Day carries the factor for awning, but that it is prevented from operating in the cross by an inhibitor which is closely linked with the factor for yellow color in the Sixty-Day variety. He attributed the production of awns in the first generation to the extent to which this inhibitor (I), is dominant over its normal allelomorph (i), which in turn is probably dependent to a large extent on environmental factors. He believes that environment influences the production of awns and states that, though experimental evidence is lacking, increased moisture and fertility of the soil tend to decrease their number. According to Fraser, the variety Sixty-Day would have the genetic formula for color rryyYY as contrasted with the formula RRYYyy of the variety Burt. He states further:

> Other workers have shown that the variety Sixty-Day carries with it a factor which inhibits the production of awns, which factor is closely linked with the factor for yellow color. Because of the yellow in the variety Burt, which carries no inhibitor, the inhibitory effect of the Sixty-Day factor was obscured.

Fraser says that considerable variation in kernel color is to be noticed even within the same pure line during different seasons or under strikingly different environments. He speaks of Sixty-Day as being a yellow variety and found white F_2 plants which failed to breed true in F_3. The difficulty of making exact color classification due to gradation is also pointed out. Linkage was observed between the fully awned condition, the presence of midlength basal hairs, and the Burt (sterilis) type of articulation.

CHARACTERS OF THE KHERSON SPIKELET

A brief description of the oat spikelet is given to make clear the discussion of the experiments which follow. The principal spikelet characters studied, as in previous similar investigations by Coffman, Parker, and Quisenberry (*4*), were spikelet disarticulation, floret disjunction, basal hairs, awns, and lemma color.[5]

The oat spikelet is borne on the end of the pedicel, terminating in the lower segment of the rachilla. Each spikelet contains two or more florets, of which usually only the two lowest are fertile, the lower one of the two being the larger and longer. The outer or empty glumes are thin, membranous, broadly lanceolate, pointed, glabrous, and broadly arched. The upper is a little longer than the lower and both exceed the lemma or flowering glume in length, except in the hull-less or naked group. There are no varieties bearing exclusively one, two, or three kernels per spikelet. Two or more usually occur and may or may not be separated in threshing. The florets are connected by the clavate segments of the jointed rachilla, each segment of which supports a single floret.

SPIKELET DISARTICULATION

The separation of the spikelet from the plant by disarticulation at the juncture of the lower floret and its supporting rachilla segment has been fully discussed in the previous paper on the Burt oat (*4*). In the present study only two distinct forms of lemma base resulting from spikelet disarticulation were recognized. The oval smooth-edged and rather prominent cavity or scar resulting from abscission, usually found in oat kernels of the Red Rustproof type, was not observed in this study of Kherson. In the present study, therefore, spikelet disarticulation was classed as by semiabscission and by fracture. The pointed form of base resulting from fracture is commonly associated with oats of the *Avena sativa* group. The term semiabscission was used for those kernels which showed a slight or poorly developed basal cavity resulting partly from abscission and partly from fracture.

FLORET DISJUNCTION

The manner of separation of the kernels of the spikelet varies with the species. In some species, as in *Avena fatua* and its derivatives, disjunction of the upper floret from its supporting rachilla segment takes place in approximately the same manner as does that of the spikelet. In *Avena sterilis* and its derivatives the rachilla and the lemma of the upper kernel are solidly grown together; the kernels do not

[5] For assistance in determining the morphologic characters of the oat spikelet and for the terminology used the writers are greatly indebted to C. R. Ball, senior agronomist in charge of Cereal Investigations.

separate readily in threshing, but the rachilla segment tears away at or near its base. At other times disjunction may result by the connecting segment splitting lengthwise or breaking at or near the mid-point.

Floret disjunction in this study was described as resulting by disarticulation when the separation left the rachilla segment attached to the face of the lower floret; by heterofracture when the rachilla segment broke at or near the mid-point, making exact classification in either of the other classes impossible; and by basifracture when the rachilla broke off at the base and remained attached to the second floret.

BASAL HAIRS

Most species of wild oats are characterized by hairiness of the lemma, callus, and rachilla. The callus often bears more or less conspicuous hairs or bristles, usually conveniently called basal hairs. Their presence may be observed readily without magnification. These hairs vary in number and length. Different authors have classified them in different ways, but all have used the length or number or combinations of these in making their classifications.

In the Kherson variety all hairs are short, with but few exceptions. On an occasional individual they might be termed midlength, but none observed were of sufficient length to be classed as long. As a result classification of basal hairs in the present study is based almost entirely on numbers of hairs. The occasional kernel with midlength hairs was arbitrarily thrown into the class with short hairs. All gradations from the very shortest hairs visible to the eye up to those of midlength were observed. In this study of Kherson the basal hairs were described as abundant, few, and absent.

AWNS

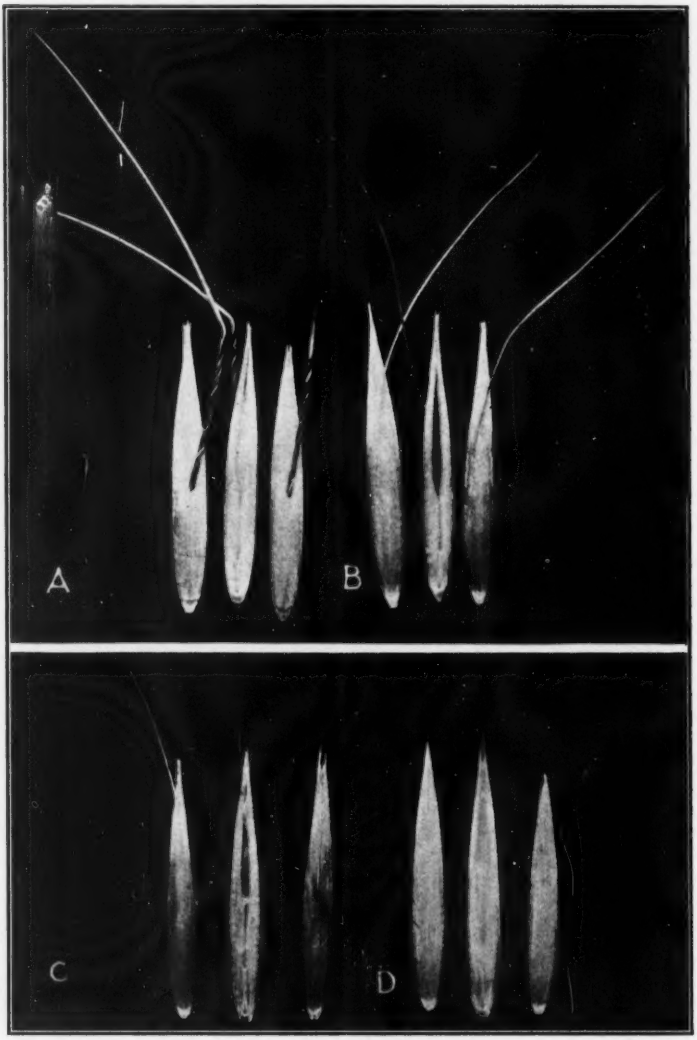
In Avena the awn is an extension of the midrib of the lemma arising from the epidermis at a point usually slightly above the middle of the dorsal surface of the kernel. In the various wild forms awns also occur on the second and third kernels. In such forms the awn usually is stout and long and the basal portion strongly twisted in a clockwise direction. The upper portion usually is bent or geniculate. In most of our cultivated varieties the awn occurs on only the lower kernel of the spikelet, which may be twisted or nontwisted and straight. In practically all the varieties of *Avena sativa* the awn occurs only on the lower lemma, and there are some varieties in which awns occur only occasionally or rarely even on the lower floret. In the varieties of *A. byzantina* awns often occur on both florets, and in the less variable varieties such as Red Rustproof and Red Algerian the awn usually is straight and rarely twisted. Trabut (*22*, *23*) observed a series of oat forms ranging from the wild red oat, *A. sterilis*, to the cultivated red oat which he called *A. sterilis culta*, and noted gradual reduction in the number of awns per spikelet and in the amount of twisting and geniculation. The occurrence of numerous twisted geniculate awns in cultivated oats is believed by some to indicate degeneracy resulting primarily from an unfavorable environment.

Various authors have used different terms to describe the nature of the awn. Etheridge (*5*) used the following terms: Twisted geniculate, strong, and weak. Fraser (*6*) in his studies of the inheritance of what he called the weak awn in certain oat crosses used the terms strong, intermediate, and weak to designate different awn types.

The following terms, indicating four classes, have been used in the present investigations: Twisted; nontwisted, long; nontwisted, short; and absent (awnless) (pl. 2). While the twisted geniculate awn usually is associated with wild forms, some cultivated varieties, such as Swedish Select, frequently show this type of awn to a marked degree. In the present study all awns showing some twisting were classed as twisted, regardless of the degree of geniculation. The nontwisted long awns often were as long as the twisted awns but were never twisted. The nontwisted short awns varied from approximately 15 mm. in length to mere bristlelike appendages.

LEMMA COLOR

In oat varieties the lemma varies in color. The principal colors recognized in descriptions of oat lemmas are black, red, gray, yellow, and white. Lemma colors in the Kherson variety were described in this study as reddish yellow or orange, yellow, and white. Lemmas called reddish yellow are of a dark orange or reddish color. The yellow class included all lemmas showing yellow color and varied from a rich cream to dark lemon-yellow. Lemmas classed as white were of an ivory or light cream color. Pure white lemmas probably do not exist in oats.



Awn types of Kherson oat

A. Twisted
B. Nontwisted long
C. Nontwisted short
D. Absent (awnless)

EXPERIMENTAL METHODS

The review of selection and other experiments has shown conclusively that the Kherson variety contains different types. The experiments described in this study were started at the Akron Field Station in 1921 to obtain information on the genetic constitution of Kherson, particularly with regard to certain spikelet and floret characters.

Kernels used in starting this study were selected singly from a bulk sample of Kherson oat, C. I. No. 459,[6] grown at the Akron Field Station in 1920. The kernels were classified and described by the system outlined by Coffman, Parker, and Quisenberry (*4*) in studies of the Burt oat.

The same general system in choosing seed and in planting was used each year. In all cases the crop was grown in the screened breeding garden at the Akron Field Station. In making the original seedings, kernels having an identical classification were sown together as a group. About 125 kernels were sown in 1921. The kernels were spaced at 3-inch intervals in rows 10 inches apart. The seed was sown on May 12 and the seedlings emerged May 21. The date of heading of each plant was recorded on a tag attached to the plant. Some plants did not mature seed because of unfavorable weather conditions.

The different plants showed considerable variation in time of heading and ripening. The earliest plants started to head July 2, while the latest date of heading was July 20. Most of the plants headed between July 10 and 16. At harvest the plants were pulled, and those of each group were tied together and stored. Later, each plant of the group was numbered, and the height of culms, number of culms, number of panicles, length of main panicle, and date of heading were recorded.

The primary floret in the spikelets, rather than the plant, was used as the unit throughout this study. In 1921 each of the primary florets from the main panicle of each plant was described. In succeeding years 25 florets per plant were described, and where the main panicle contained less than 25 spikelets more than one panicle on the same plant was used in order to obtain a sufficient number for accurate classification. The characters recorded were the same as those used in describing the original seed.

All of the distinct characters and, so far as practicable, all of the different combinations of these characters were included in the 1922 studies. In making the selections for seeding in 1922 there were sown not less than 5 nor more than 10 kernels having the same classification and from any one plant. In a few cases two groups of five kernels each from a single parent plant were sown. In such cases these groups differed in one or more characters, e. g., group 34 and group 35 both came from plant 8 of the 1921 crop (plant 8, group 14). Kernels in group 34 bore long awns in 1921, while those in group 35 were awnless.

About 250 kernels were sown in the 1922 experiments. The seed was sown April 22 and the plants emerged May 5. An excellent stand was obtained and the plants made rapid growth. As the season was dry, it was necessary to irrigate them several times.

In 1923 20 groups of kernels were sown. The seed was sown on May 7 and the plants emerged May 15. Excellent stands were obtained and the plants in most rows made very satisfactory growth.

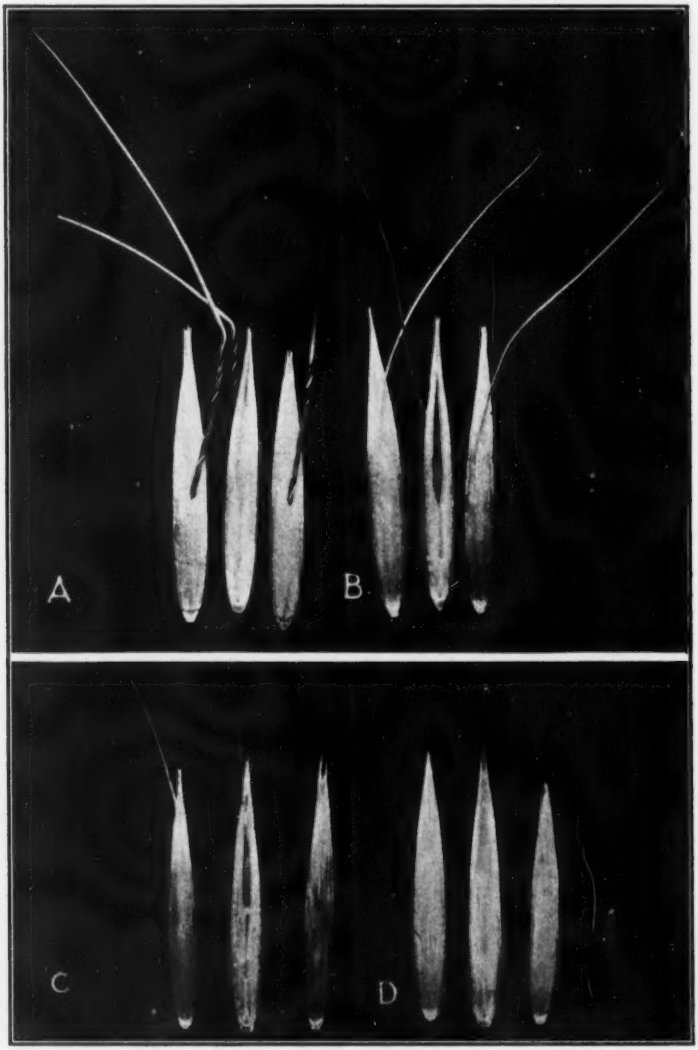
EXPERIMENTAL RESULTS

About 7,000 kernels were described in the course of this experiment, and it is impracticable to include more than a general summary of the data obtained. In discussing the results the characters studied have been considered separately.

SPIKELET DISARTICULATION

In these experiments no florets were found which had a prominent basal cavity or scar resulting from disarticulation by abscission, such as is characteristic of *Avena sterilis*, *A. fatua*, and some varieties of *A. byzantina*. Should kernels of this type occur in the Kherson oat, it might well be considered evidence of mechanical mixture or of hybridization. Only two methods of spikelet disarticulation were observed in Kherson. These were semiabscission, resulting in a slight or indistinct cavity, and fracture, resulting in a rough surface with no visible scar. The data obtained in 1921, 1922, and 1923 on the inheritance of spikelet disarticulation are shown in Table I. It appears evident that heritable variations exist in the method of spikelet disarticulation of different pedigreed strains of Kherson oat. Apparently a strong tendency exists for disarticulation by semiabscission and by fracture to be transmitted to the progeny in a high proportion of cases.

[6] Accession number of the Office of Cereal Investigations.



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[6] Accession number of the Office of Cereal Investigations.

TABLE I.—*Inheritance of spikelet disarticulation in strains of the Kherson oat grown at the Akron Field Station, Akron, Colo., in 1921, 1922, and 1923*

DATA FOR 1921

Spikelet disarticulation of parent and group number	Spikelet disarticulation in progeny			
	Number of kernels disarticulating by—		Percentage of kernels disarticulating by—	
	Semiabscission	Fracture	Semiabscission	Fracture
Semiabscission:				
4	1	18	5.3	94.7
5	124	13	90.5	9.5
12	55	55	50.0	50.0
All groups	180	86	67.7	32.3
Fracture:				
1	-----	86	-----	100.0
2	25	53	32.1	67.9
3	5	8	38.5	61.5
6	23	40	36.5	63.5
7	31	107	22.5	77.5
8	42	28	60.0	40.0
9	-----	71	-----	100.0
10	-----	37	-----	100.0
11	-----	42	-----	100.0
13	8	54	12.9	87.1
14	112	78	58.9	41.1
15	34	18	65.4	34.6
All groups	280	622	31.0	69.0

DATA FOR 1922

Semiabscission:				
6	38	36	51.4	48.6
7	17	55	23.6	76.4
8	50	107	31.8	68.2
9	84	1	98.8	1.2
10	35	34	50.7	49.3
11	23	57	28.8	71.2
14	20	10	66.7	33.3
15	25	72	25.8	74.2
22	80	20	80.0	20.0
23	52	12	81.2	18.8
24	68	3	95.8	4.2
32	78	2	97.5	2.5
33	58	17	77.3	22.7
34	119	5	96.0	4.0
35	58	-----	100.0	-----
37	49	32	60.5	39.5
40	97	33	74.6	25.4
41	66	9	88.0	12.0
All groups	1,017	505	66.8	33.2
Fracture:				
1	-----	223	-----	100.0
2	-----	105	-----	100.0
3	-----	64	-----	100.0
4	4	80	4.8	95.2

TABLE I.—*Inheritance of spikelet disarticulation in strains of the Kherson oat grown at the Akron Field Station, Akron, Colo., in 1921, 1922, and 1923*—Continued

DATA FOR 1922—Continued

Spikelet disarticulation of parent and group number	Spikelet disarticulation in progeny			
	Number of kernels disarticulating by—		Percentage of kernels disarticulating by—	
	Semiabscission	Fracture	Semiabscission	Fracture
Fracture—Continued.				
5	61	44	58.1	41.9
12	3	97	3.0	97.0
13	73	122	37.4	62.6
16	-----	26	-----	100.0
17	66	50	56.9	43.1
18	5	108	4.4	95.6
19	3	64	4.5	95.5
20	29	57	33.7	66.3
25	34	66	34.0	66.0
26	40	38	51.3	48.7
27	-----	56	-----	100.0
28	-----	127	-----	100.0
29	16	57	21.9	78.1
30	16	59	21.3	78.7
31	14	102	12.1	87.9
38	-----	30	-----	100.0
39	-----	17	-----	100.0
All groups	364	1,592	18.6	81.4

DATA FOR 1923

Semiabscission:				
4	2	123	1.6	98.4
5	93	4	95.9	4.1
10	80	45	64.0	36.0
11	118	7	94.4	5.6
15	37	15	71.2	28.8
16	75	4	94.9	5.1
18	112	-----	100.0	-----
19	100	-----	100.0	-----
20	78	-----	100.0	-----
All groups	695	198	77.8	22.2
Fracture:				
1	-----	93	-----	100.0
2	91	34	72.8	27.2
3	36	66	35.3	64.7
6	18	51	26.1	73.9
7	-----	52	-----	100.0
8	-----	136	-----	100.0
9	5	133	3.6	96.4
12	-----	109	-----	100.0
13	-----	85	-----	100.0
14	2	41	4.7	95.3
17	-----	125	-----	100.0
All groups	152	925	14.1	85.9

In 1921 parental florets disarticulating by semiabscission produced progeny of which two-thirds disarticulated by semiabscission and one-third by fracture. Parental florets disarticulating by fracture produced progenies in 1921 of which one-third disarticulated by semiabscission and two-thirds by fracture. The results obtained in 1921 indicate that a definite relation exists between parent and progeny in spikelet disarticulation. Each parental type produced a much larger percentage of progeny spikelets of its own kind of disarticulation than of the other type.

The 1922 data on the inheritance of spikelet disarticulation supported the conclusions drawn from the 1921 data on the inheritance of this character in Kherson. Eighteen progeny groups were grown in 1922 from parental florets disarticulating by semiabscission. Approximately 67 per cent of the progeny disarticulated in the same way. In only 4 of the 18 progeny groups was less than 50 per cent of the spikelet disarticulation by semiabscission, while in 5 strains more than 90 per cent, and in 1 group all progeny, were so classified.

Spikelets in which disarticulation was by fracture produced progenies in 1922 of which 81.4 per cent disarticulated by fracture and 18.6 per cent by semiabscission. The relation between parent and progeny for this character appears to be a definite one. In 8 of 21 groups sown from parental spikelets disarticulating by fracture spikelet disarticulation in all progeny was by fracture, while in only 3 of the other 13 groups did less than 50 per cent of the progeny separate by fracture. From these data it seems evident that two types of spikelet disarticulation exist in the Kherson variety. Both of these appear to be heritable to a large extent. It appears possible to isolate by selection pure-breeding lines of either type. Strains breeding true for spikelet disarticulation by fracture appear to be more numerous in Kherson than are those in which spikelet disarticulation is by semiabscission. It is impossible to determine the genetic constitution of Kherson on the basis of the data presented, but it appears evident that at least two factors are involved in the inheritance of spikelet disarticulation. The two methods of disarticulation in Kherson oat are shown in Plate 3.

Of the 11 progeny groups grown in 1923 from parental kernels in which the spikelet disarticulated by fracture, 6 bred true and 2 groups produced progeny of which more than 95 per cent were like the parent. One group produced progeny of which nearly three-fourths disarticulated by semiabscission and one-fourth by fracture. Approximately 65 and 74 per cent, respectively, of the two remaining groups disarticulated the same in progeny as in parent.

Of the 9 groups of kernels in which spikelet disarticulation in the 1922 parental kernels was by semiabscission, 1 group produced progeny nearly all of which disarticulated by fracture, 2 produced progeny of which about 64 and 71 per cent, respectively, were of the parental description, 3 produced progeny of which approximately 95 per cent was like the parent, and in 3 groups all progeny were like the parent.

As a whole in 1923 spikelets in which disarticulation was by semiabscission produced progenies of which 77.8 per cent also disarticulated by semiabscission and 22.2 per cent by fracture. Of the parental kernels in which disarticulation was by fracture 85.9 per cent of the progeny was similar, only 14.1 per cent disarticulating by semiabscission. Compared with the data obtained the two previous seasons, progress toward homozygosity is clearly shown.

FLORET DISJUNCTION

Disjunction of the second florets from their supporting rachilla segments is one of the most important characters studied, as it is fundamental in the classification of Avena. The data on this character for 1921, 1922, and 1923 are shown in Table II. The floret disjunction in the 1921 crop was predominantly by disarticulation, although approximately 20 per cent of the progeny disjoined by heterofracture or by basifracture. Except for the 1922 data, it might have been believed that Kherson was heterozygous for floret disjunction. The 1922 and 1923 data are similar and show conclusively that the second florets of the Kherson variety separate by disarticulation, the common method in the species *Avena sativa*.

(For explanatory legend see p. 1073)

TABLE II.—*Inheritance of floret disjunction in strains of the Kherson oat grown at the Akron Field Station, Akron, Colo., in 1921, 1922, and 1923*

DATA FOR 1921

Floret disjunction of parent and group number	Floret disjunction in progeny					
	Number of kernels disjoining by—			Percentage of kernels disjoining by—		
	Basifracture	Heterofracture	Disarticulation	Basifracture	Heterofracture	Disarticulation
Disarticulation:						
1	1	10	75	1.2	11.6	87.2
2	2	34	42	2.6	43.6	53.8
3	1	1	11	7.7	7.7	84.6
4	----	3	16	-----	15.8	84.2
5	9	27	101	6.6	19.7	73.7
6	1	11	51	1.6	17.5	80.9
7	3	30	105	2.2	21.7	76.1
8	1	7	62	1.4	10.0	88.6
9	2	5	64	2.8	7.1	90.1
10	1	4	32	2.7	10.8	86.5
11	----	8	34	-----	19.0	81.0
12	2	27	81	1.8	24.6	73.6
13	1	7	54	1.6	11.3	87.1
14	1	29	160	.5	15.3	84.2
15	1	3	48	1.9	5.8	92.3
All groups	26	206	936	2.2	17.7	80.1

DATA FOR 1922

Heterofracture:						
33	----	6	69	-----	8.0	92.0
Disarticulation:						
1	1	18	204	0.4	8.1	91.5
2	----	3	102	-----	2.9	97.1
3	----	2	62	-----	3.1	96.9
4	----	2	82	-----	2.4	97.6
5	----	2	103	-----	1.9	98.1
6	----	19	55	-----	25.7	74.3
7	----	3	69	-----	4.2	95.8
8	----	2	155	-----	1.3	98.7
9	----	15	70	-----	17.6	82.4
10	----	----	69	-----	-----	100.0
11	----	----	80	-----	-----	100.0
12	----	5	95	-----	5.0	95.0
13	----	9	91	-----	9.0	91.0
14	----	----	30	-----	-----	100.0
15	----	3	94	-----	3.1	96.9
16	----	----	26	-----	-----	100.0
17	1	15	100	.9	12.9	86.2
18	----	10	103	-----	8.8	91.2
19	----	7	60	-----	10.4	89.6
20	----	13	72	-----	15.3	84.7
22	----	5	95	-----	5.0	95.0
23	----	6	58	-----	9.4	90.6
24	1	10	60	1.4	14.1	84.5
25	----	6	95	-----	5.9	94.1
26	----	8	70	-----	10.3	89.7

TABLE II.—*Inheritance of floret disjunction in strains of the Kherson oat grown at the Akron Field Station, Akron, Colo., in 1921, 1922, and 1923*—Continued

DATA FOR 1922—Continued

Floret disjunction of parent and group number	Floret disjunction in progeny					
	Number of kernels disjoining by—			Percentage of kernels disjoining by—		
	Basifracture	Heterofracture	Disarticulation	Basifracture	Heterofracture	Disarticulation
Disarticulation—Continued.						
27	----	----	56	-----	-----	100.0
28	2	9	116	1.6	7.1	91.3
29	----	10	63	-----	13.7	86.3
30	1	7	67	1.4	9.3	89.3
31	----	7	109	-----	6.0	94.0
32	1	8	71	1.3	10.0	88.7
34	----	3	121	-----	2.4	97.6
35	----	4	54	-----	6.9	93.1
37	1	9	71	1.2	11.1	87.7
38	----	----	30	-----	-----	100.0
39	----	----	17	-----	-----	100.0
40	----	11	119	-----	8.5	91.5
41	----	1	74	-----	1.3	98.7
All groups	8	232	3,068	.3	7.0	92.7

DATA FOR 1923

Heterofracture:						
3	----	28	74	-----	27.5	72.5
15	----	2	50	-----	3.8	96.2
All groups	----	30	124	-----	19.5	80.5
Disarticulation:						
1	----	----	93	-----	-----	100.0
2	----	9	116	-----	7.2	92.8
4	1	4	120	0.8	3.2	96.0
5	----	10	87	-----	10.3	89.7
6	----	8	61	-----	11.6	88.4
7	----	----	52	-----	-----	100.0
8	----	4	132	-----	2.9	97.1
9	----	6	132	-----	4.3	95.7
10	1	9	115	.8	7.2	92.0
11	1	13	111	.8	10.4	88.8
12	----	12	97	-----	11.0	89.0
13	----	4	81	-----	4.7	95.3
14	----	1	42	-----	2.3	97.7
16	----	10	69	-----	12.7	87.3
17	----	5	120	-----	4.0	96.0
18	----	1	111	-----	.9	99.1
19	----	3	97	-----	3.0	97.0
20	----	----	78	-----	-----	100.0
All groups	3	99	1,714	.2	5.5	94.3

EXPLANATORY LEGEND FOR PLATE 3

Spikelet disarticulation, floret disjunction, and basal hairs of Kherson oat

A. Spikelet disarticulation by fracture, floret disjunction by disarticulation, basal hairs absent
B. Spikelet disarticulation by semiabscission, floret disjunction by disarticulation, basal hairs abundant
C. Spikelet disarticulation by semiabscission, floret disjunction by heterofracture, basal hairs few

It is reasonable to assume that the comparatively small percentage of kernels in which floret disjunction was by basifracture and by heterofracture in all years can be accounted for by chance variations or as due to accidental causes in the breaking apart of the two kernels of the spikelet rather than to a hereditary cause. It is believed, therefore, that these data show conclusively that the Kherson oat used in these experiments belongs to the *Avena sativa* group in which floret disjunction usually is by disarticulation and that it contains few, if any, strains in which floret disjunction is by basifracture, as in the *A. sterilis* group. The different methods of floret disjunction are shown in Plates 3 and 4.

BASAL HAIRS

The results obtained on the inheritance of basal hairs are presented in Table III. These data show that parental florets classed as having few basal hairs produced progeny in 1921 of which about three-fourths had either few or abundant basal hairs and about one-fourth had the basal hairs absent. Parental florets with hairs absent produced progenies of which only about 40 per cent had hairs absent, while over 60 per cent had basal hairs present. These data indicate that a tendency exists for parental kernels having basal hairs to produce progeny having basal hairs. The fact that in 1921 parental kernels without hairs produced in many cases progeny having basal hairs either few or abundant may be accounted for by the fact that the original material was machine-threshed. As a result some parental kernels which originally bore basal hairs may have had them rubbed off in threshing (Table III).

The 1922 data show that 14 of the 25 groups of parental kernels described as having few basal hairs produced progeny largely or wholly of that description, one group having all progeny like the parents. In 9 of the remaining 11 groups more progeny kernels had basal hairs absent than bore few basal hairs, 3 of these groups showing no kernels with such hairs. In 2 groups about half of the progeny were of each class.

TABLE III.—*Inheritance of basal hairs in strains of the Kherson oat grown at the Akron Field Station, Akron, Colo., in 1921, 1922, and 1923*

DATA FOR 1921

Basal hairs of parent and group number	Basal hairs in progeny					
	Number of kernels having hairs			Percentage of kernels having hairs		
	Abundant	Few	Absent	Abundant	Few	Absent
Few:						
4	----	14	5	----	73.7	26.3
6	3	44	16	4.8	69.8	25.4
9	----	40	31	----	56.3	43.7
10	11	22	4	29.7	59.5	10.8
12	----	87	23	----	79.1	20.9
15	----	52	----	----	100.0	----
All groups	14	259	79	4.0	73.6	22.4
Absent:						
1	----	42	44	----	48.8	51.2
2	2	48	28	2.6	61.5	35.9
3	----	3	10	----	23.1	76.9
5	8	68	61	5.9	49.6	44.5
7	4	55	79	2.9	39.9	57.2
8	----	57	13	----	81.4	18.6
11	----	11	31	----	26.2	73.8
13	----	42	20	----	67.7	32.3
14	----	155	35	----	81.6	18.4
All groups	14	481	321	1.7	59.0	39.3

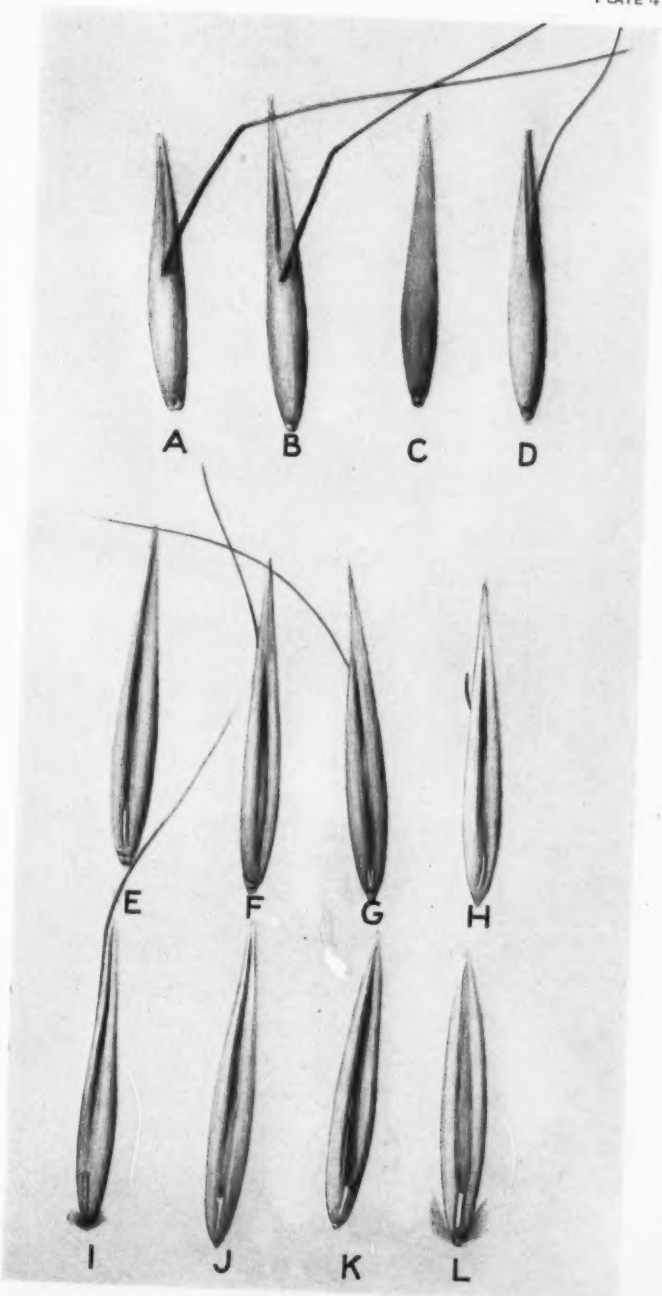
EXPLANATORY LEGEND FOR PLATE 4

Description of lemma color and other characters in Kherson florets

A. Yellowish white, basal hairs absent, awn twisted
B. Yellow, basal hairs absent, awn twisted
C. Reddish yellow, basal hairs absent, awn absent
D. White, basal hairs absent, awn nontwisted long
E. Yellowish white, spikelet disarticulation by fracture, floret disjunction by disarticulation
F. Yellow, spikelet disarticulation by fracture, floret disjunction by basifracture
G. Reddish yellow, spikelet disarticulation by fracture, floret disjunction by heterofracture, basal hairs absent, awn nontwisted long
H. White, spikelet disarticulation by fracture, floret disjunction by heterofracture, basal hairs absent, awn nontwisted short
I. Yellowish white, spikelet disarticulation by fracture, floret disjunction by disarticulation, basal hairs few, awn nontwisted long
J. Yellow, spikelet disarticulation by fracture, floret disjunction by disarticulation, basal hairs absent, awn absent
K. White, spikelet disarticulation by fracture, floret disjunction by disarticulation, basal hairs absent, awn absent
L. White, spikelet disarticulation by fracture, floret disjunction by disarticulation, basal hairs abundant, awn absent

Variation in the Kherson Oat at Akron, Colo.

PLATE 4



Ab

Abu

Few

TABLE III.—*Inheritance of basal hairs in strains of the Kherson oat grown at the Akron Field Station, Akron, Colo., in 1921, 1922, and 1923*—Continued

DATA FOR 1922

Basal hairs of parent and group number	Basal hairs in progeny					
	Number of kernels having hairs			Percentage of kernels having hairs		
	Abundant	Few	Absent	Abundant	Few	Absent
Few:						
2	----	14	91	----	13.3	86.7
3	----	9	55	----	14.1	85.9
5	----	58	47	----	55.2	44.8
6	----	38	36	----	51.4	48.6
7	----	----	72	----	----	100.0
9	----	32	53	----	37.6	62.4
10	----	----	99	----	----	100.0
13	----	69	131	----	34.5	66.5
14	----	5	25	----	16.7	83.3
15	----	----	97	----	----	100.0
17	24	81	11	20.7	69.8	9.5
18	----	9	104	----	8.0	92.0
22	----	84	16	----	84.0	16.0
23	----	62	2	----	96.9	3.1
24	----	70	1	----	98.6	1.4
25	----	90	10	----	90.0	10.0
26	----	63	15	----	80.8	19.2
29	3	52	18	4.1	71.2	24.7
30	----	51	24	----	68.0	32.0
31	----	85	31	----	73.3	26.7
32	----	78	2	----	97.5	2.5
33	----	73	2	----	97.3	2.7
34	----	124	----	----	100.0	----
35	----	55	3	----	94.8	5.2
37	----	76	5	----	93.8	6.2
All groups	27	1,278	920	1.2	57.4	41.4
Absent:						
1	----	5	218	----	2.2	97.8
4	----	22	62	----	26.2	73.8
8	----	3	154	----	1.9	98.1
11	4	2	74	5.0	2.5	92.5
12	----	35	65	----	35.0	65.0
16	----	2	24	----	7.7	92.3
19	----	7	60	----	10.4	89.6
20	----	30	56	----	34.9	65.1
27	----	----	56	----	----	100.0
28	----	----	127	----	----	100.0
38	----	2	28	----	6.7	93.3
39	----	----	17	----	----	100.0
40	----	1	129	----	.8	99.2
41	----	----	75	----	----	100.0
All groups	4	109	1,145	.3	8.7	91.0

DATA FOR 1923

Abundant:						
5	----	107	18	----	85.6	14.4
Few:						
11	----	116	9	----	92.8	7.2
14	----	25	18	----	58.1	41.9
15	----	44	8	----	84.6	15.4
16	----	78	1	----	98.7	1.3
18	----	112	----	----	100.0	----
19	----	100	----	----	100.0	----
20	----	53	25	----	67.9	32.1
All groups	----	528	61	----	89.6	10.4

TABLE III.—*Inheritance of basal hairs in strains of the Kherson oat grown at the Akron Field Station, Akron, Colo., in 1921, 1922, and 1923*—Continued

DATA FOR 1923—Continued

Basal hairs of parent and group number	Basal hairs in progeny					
	Number of kernels having hairs			Percentage of kernels having hairs		
	Abundant	Few	Absent	Abundant	Few	Absent
Absent:						
1	----	12	81	----	12.9	87.1
2	----	86	39	----	68.8	31.2
3	----	39	63	----	38.2	61.8
4	----	8	117	----	6.4	93.6
5	----	47	50	----	48.5	51.5
6	----	26	43	----	37.7	62.3
7	----	11	41	----	21.2	78.8
8	----	10	126	----	7.4	92.6
9	----	9	129	----	6.5	93.5
12	----	5	104	----	4.6	95.4
13	----	39	46	----	45.9	54.1
17	----	----	125	----	----	100.0
All groups	----	292	964	----	23.2	76.8

Of the 14 groups of the 1922 crop having parental kernels with basal hairs absent all progenies in four groups had no hairs. In only four groups were found florets having basal hairs to any considerable degree. This shows that a strong tendency exists for parental kernels without hairs to produce progeny of that description, while parental kernels with hairs show a marked tendency to produce progeny which segregate into the few and absent classes for basal hairs.

The comparatively few kernels which were described as having abundant basal hairs in this study may easily be accounted for as chance variations in all cases. There seemed to be one exception to this tendency, group 17 of the 1922 crop, but the results obtained in 1923 indicated that these few kernels also were due to chance variation and not to any heritable difference.

The data obtained in 1923 in the study of basal hairs in progeny of kernels bearing few hairs indicate that this character is more definitely inherited than was shown by similar studies in previous years. Between 85 and 90 per cent of the progeny from parental kernels bearing hairs was described as bearing hairs. However, in 11 of the 12 groups in which the parental kernels were described as having no hairs some progeny kernels were pro-

duced which bore a few hairs. Although, in 1922, 91 per cent of the progeny of kernels with hairs absent was described as without hairs, in 1923 only 76.8 per cent of the progeny of parental kernels without hairs was so described. The fluctuations in the percentages of true breeding progeny from parental kernels described as having basal hairs absent probably indicates that this character is influenced by environmental or physiological factors.

The results, however, apparently indicate the possibility of isolating strains of Kherson oats which will breed comparatively pure for few as well as for no basal hairs. Presumably pure-breeding strains having few basal hairs are as numerous in the Kherson variety as grown at Akron as those having no basal hairs. The variation in length and abundance of basal hairs found in Kherson oats is shown in Plates 2 and 4.

AWNS

The present study was conducted chiefly to obtain data on the inheritance of awning in Kherson oats. Nilsson-Ehle (*16*) apparently first stated the belief that yellow color had an inhibitory effect on awn development. The writers may be misled, but it appears that this theory possibly was advanced on the results observed by Nilsson-Ehle in a cross in which less than 25 plants with yellow kernels were produced in the F_2 generation, and of these few progeny plants some were awned. The results obtained by Surface (*20*) in his cross of *Avena fatua* with the cultivated variety Kherson did not support this theory of Nilsson-Ehle.

The results of Love and Fraser (*13*), Love and Craig (*14*), and Fraser (*6*) all fail to show conclusively that the Kherson or Sixty-Day oat contains an inhibitor for awns linked with yellow color. The failure to observe the expected inhibitory effect is explained by these writers largely on the basis that the Burt oats used in their crosses carried no such inhibitor, and thus obscured the effect of the inhibitor carried by the Kherson or Sixty-Day variety. They further explain their failure to obtain an inhibitory effect from Sixty-Day in their crosses of Sixty-Day × Burt as being partially due to climatic conditions, which may favor the production of awns in one season or cause kernels which carry the gene for awns to fail to produce awns in other seasons.

The results obtained in the present experiment do not indicate either the linkage of awnlessness and yellow color or the inhibitory effect of yellow color for the production of awns in the Kherson variety.

The data obtained in the study of awns in the Kherson oat in 1921, 1922, and 1923 are presented in Table IV.

Parental florets having twisted awns produced progenies in 1921, of which about 48 per cent had twisted, 20 per cent had nontwisted long, 2 per cent nontwisted short awns, and 32 per cent was awnless. Parental florets having nontwisted long awns produced progenies of which 7.5 per cent had twisted awns, 45.2 per cent nontwisted long, 1.4 per cent nontwisted short, and 45.9 per cent had absent awns. Awnless parental florets produced progeny of which about 90 per cent were awnless, 7 per cent had nontwisted long awns, 1.6 per cent had nontwisted short awns, and 1.8 per cent had twisted awns. The data obtained in 1921 indicated that the twisted, nontwisted long, and absent awns differed in their hereditary behavior. It appeared that the absence of awns was more constant in breeding behavior than the others and that the nontwisted long awn differs genetically from the twisted awn. Both types appeared similar in the production of florets with nontwisted short or absent awns.

Much more definite data were obtained on the inheritance of awns in Kherson oats in 1922. These data indicate that the twisted awn possibly is recessive to the nontwisted long awns and to awnlessness. Nearly 95 per cent of the progeny of parental florets having twisted awns had twisted awns, while a very few had nontwisted long or short awns, and only about 5 per cent was awnless. The studies in Burt oats by Coffman, Parker, and Quisenberry (*4*) have shown the tendency of kernels in that variety having the twisted awn to produce progeny with awns of that character or no awns at all. Parental kernels of Kherson oats having nontwisted long awns produced progeny in 1922 of which 64.9 per cent had nontwisted long awns, 12 per cent had twisted awns, 10.1 per cent had nontwisted short awns, and 13 per cent was awnless.

The failure of awnless parental kernels to produce progeny all of which were awnless has been noted by previous investigators. In the 1922 crop of Kherson oats grown at Akron 74.3 per cent of the progeny of awnless parental kernels was awnless, 5.8 per cent had nontwisted short awns, 18.7 per cent had nontwisted long awns, and 1.2 per cent had twisted awns.

TABLE IV.—*Inheritance of awns in strains of the Kherson oat grown at the Akron Field Station, Akron, Colo., in 1921, 1922, and 1923*

DATA FOR 1921

Awn of parent and group number	Awns in progeny							
	Number of kernels having awns				Percentage of kernels having awns			
	Twisted	Nontwisted		Absent	Twisted	Nontwisted		Absent
		Long	Short			Long	Short	
Twisted:								
4		8		11		42.1		57.9
5	96			41	70.1			29.9
8	61	4	3	2	87.1	5.7	4.3	2.9
12	38	35	2	35	34.6	31.8	1.8	31.8
14	31	62	6	91	16.3	32.6	3.2	47.9
15	48	2		2	92.3	3.9		3.8
All groups	274	111	11	182	47.4	19.2	1.9	31.5
Nontwisted:								
3	6	1		6	46.2	7.7		46.1
9		40	1	30		56.3	1.4	42.3
13	5	25	1	31	8.1	40.3	1.6	50.0
All groups	11	66	2	67	7.5	45.2	1.4	45.9
Absent:								
1		9	2	75		10.5	2.3	87.2
2				78				100.0
6	5	15	5	38	7.9	23.8	7.9	60.4
7		6		132		4.3		95.7
10				37				100.0
11	3	1		38	7.1	2.4		90.5
All groups	8	31	7	398	1.8	7.0	1.6	89.6

DATA FOR 1922

Twisted:								
7	65			7	90.3			9.7
8	155			2	98.7			1.3
10	69				100.0			
11	78			2	97.5			2.5
14	29			1	96.7			3.3
15	86			11	88.7			11.3
22	90	1	1	8	90.0	1.0	1.0	8.0
23	64				100.0			
34	120	1	1	2	96.8	.8	.8	1.6
37	67	2	3	9	82.7	2.5	3.7	11.1
All groups	823	4	5	42	94.1	.5	.6	4.8
Nontwisted:								
16		22	2	2		84.6	7.7	7.7
24	3	64	1	3	4.2	90.2	1.4	4.2
25	21	63	9	7	21.0	63.0	9.0	7.0
26	29	38	6	5	37.2	48.7	7.7	6.4
29		42	17	14		57.5	23.3	19.2
31	21	60	9	26	18.1	51.7	7.8	22.4
32	12	63	5		15.0	78.8	6.2	
33		74		1		98.7		1.3
38		10	20			33.3	66.7	
41	1	34	4	36	1.4	45.3	5.3	48.0
All groups	87	470	73	94	12.0	64.9	10.1	13.0

TABLE IV.—*Inheritance of awns in strains of the Kherson oat grown at the Akron Field Station, Akron, Colo., 1921, 1922, and 1923*—Continued

DATA FOR 1922—Continued

Awn of parent and group number	Awns in progeny							
	Number of kernels having awns				Percentage of kernels having awns			
	Twisted	Nontwisted		Absent	Twisted	Nontwisted		Absent
		Long	Short			Long	Short	
Absent:								
1		66	25	132		29.6	11.2	59.2
2	3	47	15	40	2.9	44.7	14.3	38.1
3				64				100.0
4				84				100.0
5				105				100.0
6	4	1		69	5.4	1.4		93.0
9	3	1		81	3.5	1.2		95.2
12			1	99			1.0	99.3
13				200				100.0
17				116				100.0
18		30	10	73		26.5	8.9	64.0
19			7	60			10.4	89.6
20	3	60	8	15	3.5	69.8	9.3	17.6
27		22	11	23		39.3	19.6	41.4
28	5	26	5	91	3.9	20.5	3.9	71.1
30		21	12	42		28.0	16.0	56.7
35	3	8	2	45	5.2	13.8	3.4	77.6
39	1	15		1	5.9	88.2		5.9
40		55	14	61		42.3	10.8	46.9
All groups	22	352	110	1,401	1.2	18.7	5.8	74.3

DATA FOR 1923

Twisted:								
4	124			1	99.2			0.8
9	137			1	99.3			.7
15	34	14	2	2	65.4	26.9	3.9	3.8
18	59	17	15	21	52.7	15.2	13.4	18.7
19	72	11	2	15	72.0	11.0	2.0	15.0
20	18	11	3	46	23.1	14.1	3.8	59.0
All groups	444	53	22	86	73.4	8.8	3.6	14.2
Nontwisted:								
1	2	29	9	53	2.2	31.2	9.7	56.9
14	8	21	11	3	18.6	48.8	25.6	7.0
16	10	66	1	2	12.7	83.5	1.3	2.5
17		18	3	104		14.4	2.4	83.2
All groups	20	134	24	162	5.9	39.4	7.1	47.6
Absent:								
2			1	124			.8	99.2
3	3		1	98	2.9		1.0	96.1
5	7	5	3	82	7.2	5.2	3.1	84.5
6				69				100.0
7			1	51			1.9	98.1
8				136				100.0
10				125				100.0
11				125				100.0
12		1	1	107		.9	.9	98.2
13		2	1	82		2.3	1.2	96.5
All groups	10	8	8	999	1.0	.8	.8	97.4

The data obtained on the inheritance of awns in the Kherson oat in 1923 were similar to those of previous seasons in many respects. Although the percentage of progeny of kernels described as bearing twisted awns was smaller in 1923 than in 1922, it was much larger than that of 1921. The breeding behavior of the kernels having nontwisted long awns was very similar in 1923 to that of 1921, and awnless parental kernels indicated a very strong tendency to produce only awnless progeny.

The data on inheritance of awns clearly indicate that genetically three types of awns exist in the Kherson oat. All three types tend to breed true. The twisted awn appears to breed as a recessive. Possibly because of physiological influences, some kernels which carry the factor for producing this type of awn fail to produce awns at all or produce the other types. The nontwisted long awn in Kherson is much less definite in breeding behavior than is the twisted awn. The nontwisted short awn in Kherson probably results from chance variation. Its genetic constitution probably is similar to the nontwisted long awn. It appears probable that pure-breeding strains which bear long awns can be isolated from the variety. The data for each group show more clearly than do the summaries for all groups that many pure-breeding awnless strains exist in Kherson oat, although not all awnless strains breed true for that condition.

Nilsson-Ehle (*17*) has stated that external conditions may greatly influence the production of awns in cultivated oat varieties. The junior author in classification studies of oats conducted at widely separated points in the United States has observed that the number of awns in some varieties and strains varies apparently with environmental conditions. For this reason it can not be assumed that these Kherson strains would show a similar behavior for awns under a decidedly different set of conditions.

The awn types found in the present study of Kherson oats are shown in Plates 2 and 4.

LEMMA COLOR

Only three lemma colors have been recognized in this study of the Kherson variety. These colors, reddish yellow, yellow, and white, have been described previously (pl. 4). Table V presents the data on color in 1921, 1922, and 1923, and shows conclusively that the yellow color is the most stable in breeding behavior. Both of the other kernel colors tend to break up and produce more progeny described as yellow than of the other types. The distinctions between the different color classes in oats are often difficult to make, as the colors grade into one another. This is due partly to the effects of physiological influences, which may cause genetically white kernels to be called yellow or yellow kernels to appear either reddish yellow or white.

TABLE V.—*Inheritance of lemma color in strains of the Kherson oat grown at the Akron Field Station, Akron, Colo., in 1921, 1922, and 1923*

DATA FOR 1921

Color of parental lemmas and group number	Lemma color in progeny					
	Number of lemmas			Percentage of lemmas		
	Reddish yellow	Yellow	White	Reddish yellow	Yellow	White
Reddish yellow:						
8	3	45	12	5.0	75.0	20.0
Yellow:						
1	11	69	6	12.8	80.2	7.0
9	5	66	----	7.0	93.0	----
10	25	12	----	67.6	32.4	----
11	9	30	3	21.4	71.4	7.2
12	34	76	----	30.9	69.1	----
13	1	54	7	1.6	87.1	11.3
14	78	112	----	41.1	58.9	----
15	45	7	----	86.5	13.5	----
All groups	208	426	16	32.0	65.5	2.5
White:						
2	----	44	34	----	56.4	43.6
3	6	7	----	46.2	53.8	----
4	1	10	----	9.1	90.9	----
5	4	19	97	3.4	15.8	80.8
6	18	27	4	36.7	55.1	8.2
7	2	136	----	1.4	98.6	----
All groups	31	243	135	7.6	59.4	33.0

DATA FOR 1922

Reddish yellow:						
2	6	99	----	5.7	94.3	----
17	----	116	----	----	100.0	----
22	3	97	----	3.0	97.0	----
24	----	71	----	----	100.0	----
27	----	56	----	----	100.0	----
31	8	105	3	6.9	90.5	2.6
32	2	78	----	2.5	97.5	----
33	----	75	----	----	100.0	----
37	9	72	----	11.1	88.9	----
All groups	28	769	3	3.5	96.1	.4
Yellow:						
1	20	203	----	9.0	91.0	----
3	----	64	----	----	100.0	----
4	44	40	----	52.4	47.6	----
12	----	43	57	----	43.0	57.0
13	----	155	45	----	77.5	22.5
15	17	64	16	17.5	66.0	16.5

TABLE V.—*Inheritance of lemma color in strains of the Kherson oat grown at the Akron Field Station, Akron, Colo., in 1921, 1922, and 1923*—Con.

DATA FOR 1922—Continued

Color of parental lemmas and group number	Lemma color in progeny					
	Number of lemmas			Percentage of lemmas		
	Reddish yellow	Yellow	White	Reddish yellow	Yellow	White
Yellow—Contd.						
16	1	25	----	3.8	96.2	----
18	11	102	----	9.7	90.3	----
19	41	26	----	61.2	38.8	----
20	2	84	----	2.3	97.7	----
23	----	64	----	----	100.0	----
25	----	100	----	----	100.0	----
26	----	78	----	----	100.0	----
28	----	127	----	----	100.0	----
29	----	73	----	----	100.0	----
30	4	71	----	5.3	94.7	----
34	31	93	----	25.0	75.0	----
35	----	58	----	----	100.0	----
38	2	28	----	6.7	93.3	----
39	----	17	----	----	100.0	----
40	----	130	----	----	100.0	----
41	----	75	----	----	100.0	----
All groups	173	1,720	118	8.6	85.5	5.9
White:						
5	----	105	----	----	100.0	----
6	42	32	----	56.8	43.2	----
7	20	37	15	27.8	51.4	20.8
8	6	81	70	3.8	51.6	44.6
9	4	55	26	4.7	64.7	30.6
10	2	54	13	2.9	78.3	18.8
11	----	34	46	----	42.5	57.5
14	12	18	----	40.0	60.0	----
All groups	86	416	170	12.8	61.9	25.3

DATA FOR 1923

Reddish yellow:						
3	----	----	102	----	----	100.0
13	----	85	----	----	100.0	----
All groups	----	85	102	----	45.5	54.5
Yellow:						
1	----	93	----	----	100.0	----
2	----	44	81	----	35.2	64.8
4	----	----	125	----	----	100.0
5	----	----	97	----	----	100.0
6	----	19	50	----	27.5	72.5
7	----	----	52	----	----	100.0
8	----	118	18	----	86.8	13.2
10	----	125	----	----	100.0	----
11	----	125	----	----	100.0	----
12	----	109	----	----	100.0	----
14	----	43	----	----	100.0	----
15	----	52	----	----	100.0	----
16	----	79	----	----	100.0	----
17	----	125	----	----	100.0	----
18	----	112	----	----	100.0	----
19	----	100	----	----	100.0	----
20	----	78	----	----	100.0	----
All groups	----	1,222	423	----	74.3	25.7
White:						
9	----	----	138	----	----	100.0

The parental groups in which the lemma color was described as reddish yellow in 1922 produced progenies of which over 96 per cent of the lemmas was yellow. White parental kernels produced progenies in which about 62 per cent of the lemmas was yellow and 13 per cent reddish yellow. Parental kernels classed as yellow produced yellow progeny very largely.

It would be difficult to explain on a factorial basis the data on lemma color shown in Table V. All classes tended to produce a high percentage of yellow kernels. Most of the reddish-yellow lemmas in Kherson apparently are due to physiological causes. The white kernels appeared unstable in breeding behavior in 1921 and 1922, as they produced many of the yellow and reddish-yellow types. In 1923, however, parental white kernels produced only white progeny. Probably many genetic yellows were incorrectly described as white in the 1921 crop, due to physiological influences. This condition is very evident in the progeny of groups 5, 6, and 14, from which no white kernels whatever were produced in 1922. The parent kernels, apparently, were simply bleached yellow.

These data indicate that at least two genetic color types exist in the Kherson oat—yellow and white. The yellow type apparently is decidedly more numerous and also less influenced by physiological factors than the white. Possibly some of the yellows are heterozygous, which would account for the occurrence of white kernels in the progenies of parental kernels described as yellow. Physiological factors may account for some of the progeny of white kernels being described as yellow and reddish yellow in 1921 and 1922.

SUMMARY

The Kherson and Sixty-Day oats are identical for all characters. Together with the pure-line selections developed from them, they constitute a very important agronomic group, occupying about 14 per cent of the oat acreage in the United States in 1919.

Several valuable selections have been made from the variety, among which Albion (Iowa No. 103), Richland (Iowa No. 105), Iowar, Nebraska No. 21, and States Pride (Wisconsin No. 7), are the most important.

The variability of the variety and the possibility of making selections from it have long been recognized.

Numerous crosses using strains of the variety have been made, and the genetic constituton of some of the result-

ant strains has been rather definitely stated. Only a few of these crosses have produced strains of any economic promise.

Spikelet disarticulation by abscission, so characteristic of Red Rustproof oats, does not occur in Kherson. Disarticulation by semiabscission breeds true in some strains, but shows apparent segregation in others. Most strains show the more or less rough and pointed base resulting from fracture, which is characteristic of *Avena sativa* varieties.

Floret disjunction in strains of Kherson oat is predominantly by disarticulation, as in *Avena sativa*, and probably is homozygous. The very small percentage of kernels showing floret disjunction either by basifracture, as in *A. sterilis*, or by heterofracture, an intermediate type, can be explained on the principle of chance variation.

Basal hairs appear exceedingly complex in their mode of inheritance. With few exceptions all basal hairs in the Kherson oat are midlength to short. Several factors apparently are involved and further study is necessary to determine their true genetic behavior.

The inheritance of awn type apparently shows no definite relation between the presence of awns and kernel color. This is contrary to the results obtained by certain other investigators. The data obtained in the present investigations indicate that the yellow color of the Kherson strain used does not carry an inhibitor for awns, as all types of awns have been found on yellow kernels. It has been shown further that it is possible to isolate yellow-kerneled strains which apparently are homozygous for certain awn types as well as for practically complete awnlessness. Several factors apparently are concerned in the production of awns in Kherson oats. Further investigations are necessary to determine the genotypic constitution of strains having different awn types and the influence of physiological factors on awn production.

Apparently only two factors for color exist in Kherson oat lemmas—viz., one for yellow and one for white. Some strains evidently are heterozygous for lemma color, but yellow is predominant, and many yellow strains are homozygous, as shown by their breeding behavior. Some white strains exist in Kherson, but they are much less numerous. Apparently physiological influences often cause genetically yellow kernels to be classed as phenotypically white kernels and vice versa.

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RELATION BETWEEN WEATHER CONDITIONS AND YIELD OF COTTON IN LOUISIANA [1]

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INTRODUCTION

This study was undertaken to discover to what degree the variations in yield of cotton may be explained on the basis of the available weather data. Obviously the yield of cotton must be greatly influenced by factors which operate prior to our being aware of their effect as measured by the resulting yield. If we may measure these factors as they occur, and then discover a statistical relation between the antecedent conditions and the subsequent yields, we are then in position to make forecasts of yield at the time the weather conditions occur. In the following discussion it will be shown that a fairly close relationship was established between the weather conditions prior to September and the subsequent final yield of cotton. The nature of these functional relations is shown in Figure 1.

Analyses of the quantitative relationship between weather factors and yields of crops have been made by several investigators. For example, H. L. Moore in 1917,[2] and more recently J. Warren Smith, of the United States Weather Bureau,[3] have both published results of such investigations. The present contribution is an extension of the methods suggested in Moore's book. A statement follows of the theoretical considerations upon which the subsequent statistical analysis was made.

FACTORS INFLUENCING YIELD

There are four major types of factors influencing yield: (1) Inherent capacity of the plant itself to bear; (2) fertility of the soil; (3) weather and length of the growing season; and (4) cultural methods applied to the crop during its growth; that is, the influence which the grower can exert to accentuate favorable, and minimize unfavorable, natural conditions.

If a State is considered as a whole, the influence of some of these factors, while continuing to be of significance in determining the long-time or trend movement in yield, is of little significance in year-to-year variations. There is great inertia in the cultural habits of the producer, for example. A new method when introduced is adopted and tried by a few, and if successful it is taken up by others the following season. Such a slow change is witnessed in the gradual introduction of the practice of spacing plants closely in the row—from 4 to 8 inches—a practice that is recommended by the United States Department of Agriculture as a means of reducing losses from weevil. The effects of such changes, even if marked in given localities, are but slight when the State is considered as a whole and the total effect on yield is so spread over a number of years that it may be considered as a long-time or "trend" change and conversely of little importance in year-to-year variations.

A similar proposition holds true for seed introduction. The shifting from one staple length to another in accordance with the premiums offered for long staple cotton will, however, probably find some reflection in yield, since a normal yield in pounds per acre for short staple is considerably greater than for long staple. Consequently, variations in yield not accounted for by weather may be considered in some degree attributable to this factor.

Soil fertility of the areas in cotton may be changed by the shifting of acreages, the opening up of new lands, and gradual exhaustion of the soil. The producer may also apply various kinds and amounts of fertilizer according to his cultural practice. A glance at Figure 1 will show that there is a distinct downward trend in yield. The bringing in of new lands less suitable for cotton growing may in part explain this trend, but it is more probable that the Mexican boll weevil has more to do with it. As in

[1] Received for publication Sept. 15, 1924; issued August, 1925.

[2] MOORE, H. L. FORECASTING THE YIELD AND THE PRICE OF COTTON. 173 p., illus. New York. 1917.

[3] SMITH, J. W. INFLUENCE OF THE WEATHER ON THE YIELD OF CROPS. Mo. Weather Rev. 50: 567-572, illus. 1922.

the case of the year-to-year changes in staple length, so the changes in the amounts of fertilizer used are of some, but probably small, importance in accounting for the variations in yield. If the bringing in of new lands has a significant effect on fertility, this too may be considered as a long-time or trend influence. Weather as a factor in yield may now be considered.

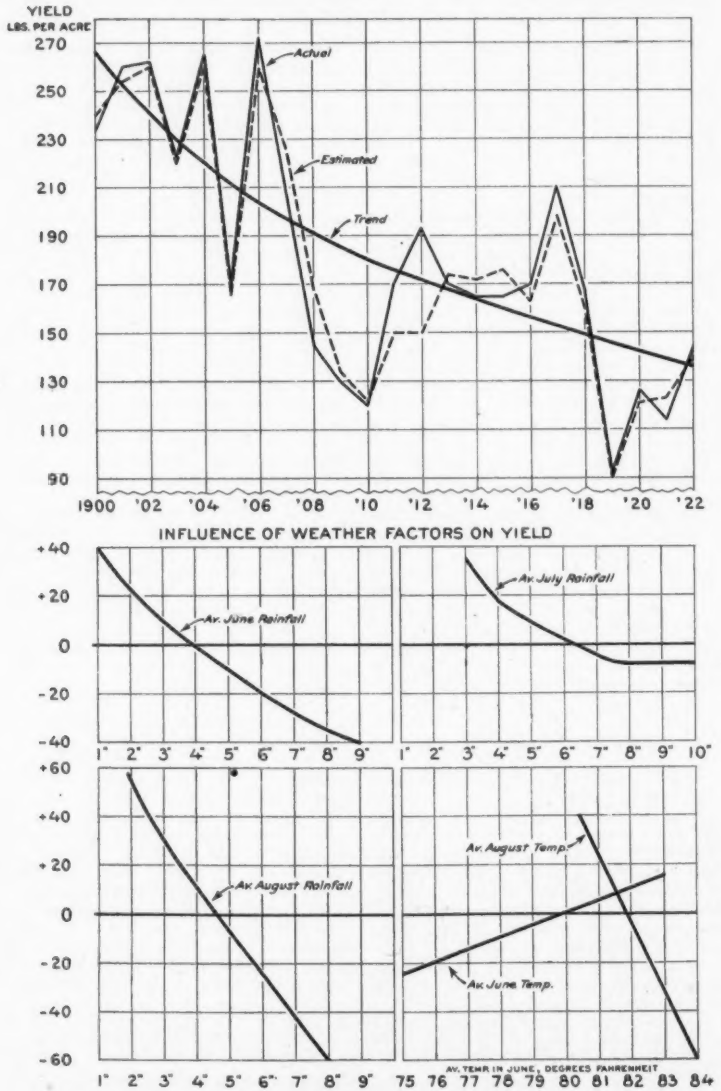

FIG. 1.—Yield of cotton in Louisiana and yield estimated from weather factors, 1900–1922

The cotton plant can not survive in a freezing temperature, and it is conceivable that a temperature could be too high. Somewhere between the extremes there must be an optimum point. There is probably also an optimum condition of rainfall. Since there is considerable variation in rainfall and temperature from one season to another, there must necessarily be considerable deviation from this optimum. As weather shows the greatest year-to-year variation of the four factors mentioned and is of influence throughout the entire State, there is presumably a relation between changes in weather conditions and changes in average yield. The attempt was accordingly made to discover this relation between weather conditions and yield, and to ascertain to what degree the latter may be explained by the former. Residual variations in yield (changes left over after the effects of weather have been eliminated) were then considered attributable to one or more of three things: (1) Errors in the original estimates of yield and weather data used; (2) an insufficient statistical expression of weather conditions; and (3) influence of the factors mentioned other than weather. As a matter of fact, these residuals were very slight, thus furnishing statistical support for the hypothesis advanced.

TABULATION OF DATA

For use in the quantitative analysis, data on yield per acre and rainfall and temperature were selected. Official figures of yield per acre of the United States Department of Agriculture were selected after comparison with the sources from which the final figures are taken. This is an expression of yield in pounds of lint cotton produced per acre.

Selection of weather data to be used was governed to a considerable extent by what is available without reworking the original Weather Bureau records. Undoubtedly, percentage of sunshine, humidity, winds, rainfall, and temperature taken for short periods of time, particularly in critical growing periods, are of importance. As only monthly data, however, are readily available over the period of time selected, 1900 to 1922, inclusive, the shortest weather period that could be used was automatically defined. Furthermore, temperature and rainfall are the only satisfactory State average weather figures covering the period. Accordingly the following series (Table I) for the State selected (Louisiana) were chosen for comparison and correlation with yield.

A number of other rainfall and temperature series were experimented with, but they showed slight relation to yield and are not included here. Table I records the original data described in the preceding.

TABLE I.—*Average rainfall and temperature for certain months and yield of lint cotton per acre, Louisiana, for the years 1900 to 1922 inclusive.*

Year	June	July	August	June	August	Yield
	Inches	*Inches*	*Inches*	*°F.*	*°F.*	*Pounds*
1900	8.40	7.11	4.59	79.3	81.4	234
1901	2.99	7.08	5.46	81.2	81.9	260
1902	1.84	4.56	3.47	81.6	84.1	262
1903	4.18	6.12	4.71	75.5	81.7	223
1904	3.89	7.17	5.19	80.0	80.2	265
1905	7.22	8.52	4.92	81.1	82.6	170
1906	3.40	7.97	2.92	81.8	82.1	272
1907	1.77	4.07	4.66	79.2	82.8	210
1908	4.10	10.61	6.61	80.6	81.3	145
1909	6.51	3.90	6.12	80.2	82.8	130
1910	7.26	7.85	4.42	78.1	82.8	120
1911	4.63	9.37	8.01	82.7	81.5	170
1912	5.67	6.63	5.89	77.3	81.3	193
1913	3.72	7.19	4.47	78.4	81.7	170
1914	2.51	7.07	7.48	83.4	80.8	165
1915	3.11	5.75	6.78	81.9	80.8	165
1916	3.89	8.00	4.49	80.5	82.0	170
1917	1.29	5.58	5.71	79.5	81.1	210
1918	3.70	3.16	6.68	82.7	81.9	167
1919	6.63	6.10	5.11	78.3	82.8	93
1920	5.21	8.18	6.61	78.7	80.5	126
1921	5.42	6.60	3.31	80.3	83.4	114
1922	5.61	5.85	5.26	80.4	81.3	144

The method of handling the described data is an extension of multiple correlation methods [4] designed by M. Ezekiel, of the Bureau of Agricultural Economics, and is briefly as follows:

By the usual methods of multiple correlation,[5] the net regression lines showing net effect of each weather factor upon the yield are plotted. The values of the dependent as obtained from the regression equation are determined, as are the residuals—plus or minus differences between the actual yield and yield estimated from regression equation. These residuals are in turn plotted against each weather factor as deviations from each of the regression lines, the lines then being curved to pass through the plotted points in so far as consistent with the hypothesis of a "smooth curve" func-

[4] EZEKIEL, M. J. B. A METHOD OF HANDLING CURVILINEAR CORRELATION FOR ANY NUMBER OF VARIABLES. Jour. Amer. Statis. Assoc. 19: 431–453, illus., 1924.

[5] TOLLEY, H. R., and EZEKIEL, M. J. B. A METHOD OF HANDLING MULTIPLE CORRELATION PROBLEMS. Jour. Amer. Statis. Assoc. 18: 993–1003. 1923.

tion. From these curves the dependents are again estimated by reading from the curve the yield value associated with each given weather value. New residuals are obtained and plotted as deviations from the regression curves, and the process is continued until the residuals can not be reduced further. It is seen that this method is one of approximation and as such is not susceptible to the mathematical demonstration of validity and probability as are many other statistical methods. On the other hand, as measured by the closeness with which the actual yield may be estimated from the independent factors and by empirical tests, the method is considerably superior. Linear correlation is not a satisfactory method of analysis when the theory predicates nonlinear relationships, that is, optimum conditions. For the purpose of obtaining the best trend line, time was treated as an independent variable in this analysis.

When the curvilinear analysis just described is completed, the net functional relationship between the weather factors and yield is described by the resulting curves. These curves are charted in Figure 1. By reading from them the yield deviations from trend (ordinates) associated with the given weather factors measured in any given season (abscissae), and by summing these readings and subtracting the constant, 2.0, an estimate of the yield may be obtained, expressed as deviation from normal or trend value. This can be done early in September, thus giving an unusually close estimate of the final yield at a comparatively early date. Such estimates were worked out for the period studied, and the curve so obtained is shown on the chart. With the omission of two years, 1911 and 1912, where there is a most pronounced recovery in the yield figure, the correlation index [6] between the actual and the estimated is unusual (0.97), the standard error of estimate being but a fourth of the standard deviation of yield from trend.

Two considerations tend to diminish the reliability of forecasts made from these curves. In the first place there are very few observations upon which to base the curves. There are about 20 years which have been used to establish five separate functional relationships. The correlation is probably in some degree due to the mere numerical probabilities of adjusting these functions to observations. This influence, however, is probably slight, since the correlation is so unusually high and since the curves represent relationships which are in accordance with the conception of what the effect of weather factors should be. For example, the curves indicate that there is generally too much rain during the June-to-August growing period, since an increase in rainfall is accompanied by a decrease in yield. This furnishes support for the proposition that an increase in rainfall increases the activity of the weevil and hence increases crop damage.

In the second place, during the first few years of the period covered there was but slight boll-weevil infestation. In 1909, however, practically all of Louisiana was infested. The weather is considered an important factor in the life of the weevil. Thus what would normally be good weather for cotton growing might be the reverse under infestation, because such weather might favor weevil propagation; that is, the influence of weather factors when operating on the cotton plant through the weevil would be different from the influence when these factors were operating directly upon the plant. The curves, then, contain the results of two mixed influences, one of which is now predominant. To avoid this mixture through shortening the period by limiting the analysis to those years subsequent to 1908 is to so greatly increase the first possibility of error mentioned as to render any curves practically invalid. But as an experiment, a linear multiple correlation coefficient was obtained for the years 1908 to 1922, inclusive, using June and August rainfall and August temperature as the independent variables. This coefficient was 0.755. It could undoubtedly have been higher if curves had been used, but it was felt that the data were insufficient to justify the use of curves. The regression equation arrived at is given below, A referring to June rainfall, E to August rainfall, and F to August temperature.

$$\text{Yield} = 919.38 - 11.43A - 0.74E - 8.69F$$

Of the three factors involved, A is the most important and E the least. The regressions are all negative, as the curves were, when derived from the longer series. This serves as a partial indication of the predominance of the weevil influence in determining the curves, and therefore encourages the placing of confidence in the curves.

[6] EZEKIEL, M. J. B. A METHOD OF HANDLING CURVILINEAR CORRELATION FOR ANY NUMBER OF VARIABLES. Jour. Amer. Statis. Assoc. 19: 431–453, illus., 1924.

RELATIVE SUSCEPTIBILITY OF SOME RUTACEOUS PLANTS TO ATTACK BY THE CITRUS-SCAB FUNGUS [1]

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In a former publication by the senior writer of this paper [2] were listed most of the commercially important citrus plants subject to scab in Florida. The present paper gives a more extensive list indicating the relative susceptibility to the disease as it occurs on its hosts in central and south Florida.

The data presented here are based on: (1) Observations made in commercial citrus nursery and grove plantings during more than seven years, viz, 1916 to 1924; (2) studies of rare forms of undetermined susceptibility closely interplanted with sour orange seedlings severely affected with scab; and (3) inoculation tests made on many rutaceous plants growing on the grounds of the field station of the United States Bureau of Plant Industry at Orlando, Fla. The method used in these inoculation tests has already been described.[3]

Citrus scab is caused by the fungus usually but erroneously referred to as *Cladosporium citri* pro tem Massee. Anna E. Jenkins,[4] assistant mycologist in the Bureau of Plant Industry, United States Department of Agriculture, has published a paper dealing with the morphology and taxonomy of this organism and has described the scab pathogene as *Sphaceloma fawcettii* n. sp.

Observations and inoculations on commercial citrus varieties have been extensive enough to be thoroughly dependable; on the noncommercial varieties and hybrids they have been limited to a small number of plants, and for that reason the general impression of relative susceptibility is given tentatively. Further observations may indicate that these hosts may be affected in a degree different from that reported herein. Many of the rutaceous plants under study are quite small and have not fruited; therefore observations were limited to occurrence of the disease on leaves and tender twigs. However, for those forms that have fruited there seems to be no difference in susceptibility of the fruit as compared with leaves and twigs.

RELATIVE SUSCEPTIBILITY TO SCAB

The results of the inoculations and observations on the relative susceptibility of many rutaceous plants to attack from the scab fungus are given in Table I.[5]

It is interesting to note that, with the exception of *Claucena lansium*, the rutaceous plants attacked by scab belong to the subtribe Citrinae. Members of only four genera, viz, Citropsis, Poncirus, Fortunella, and Citrus are known to be affected by this disease. Poncirus and Fortunella until a few years ago were regarded as members of the Citrus genus. Under conditions in central Florida, *Claucena lansium* is attacked moderately, while *Poncirus trifoliata* is only slightly affected. Only once has scab been observed on Citropsis and likewise only once has it been observed on any Fortunella species, in spite of the fact that for years they have been growing close to scab-infected grapefruit and sour orange trees. This kumquat (Fortunella) infection resulted from artificial inoculation.

At no time has scab been observed on four species of Citrus, viz, *Citrus ichangensis*, *C. medica*, *C. janos*, and *C. webberi*.

Several varities of lemon (*Citrus limonia*) are extremely liable to attack by scab, while the sweet lemon and the dwarf Chinese lemon have thus far been observed to be distinctly less susceptible to severe injury.

The Kusaie and Sour Rangpur lime (*C. aurantifolia*) are severely attacked by scab; the Tahiti lime has been found

[1] Received for publication Sept. 24, 1924; issued August, 1925.

[2] WINSTON, J. R. CITRUS SCAB: ITS CAUSE AND CONTROL. U. S. Dept. Agr. Bul. 1118, 39 p., illus. 1923.

[3] WINSTON, J. R. Op. cit., p. 23.

[4] JENKINS, A. E. THE CITRUS SCAB FUNGUS. Phytopathology 15: 99–104, illus. 1925.

[5] The botanical classification of rutaceous species and hybrids referred to in this paper follows W. T. Swingle in his articles in BAILEY, L. H. THE STANDARD CYCLOPEDIA OF HORTICULTURE. 6 v. New York. 1914. Entry under genus names.

TABLE I.—*Relative susceptibility of some rutaceous plants to citrus scab*

Botanical name	Common or variety name	Range of susceptibility				
		No infection observed	Very rarely attacked	Slightly susceptible	Moderately susceptible	Very susceptible
Family Rutaceae:						
Subfamily Citratae—						
Glycosmis pentaphylla D. C.		×				
Clausena lansium Sk.					×	
Chalcas (Murraea) exotica Mills.		×				
Tribe Citreae—						
Subtribe Aeglinae—						
Feronia limonia Sw.		×				
Feroniella lucida Sw.		×				
Aeglopsis chevalieri Sw.		×				
Aegle mamelos Cor.		×				
Chaetospermum glutinosa Sw.		×				
Balsamocitrus gabonensis Sw.		×				
Subtribe Lavanginae—						
Hesperethusa crenulata Roem.		×				
Triphasia trifolia P. Wilson.		×				
Paramignia monophylla Wight.		×				
Severinia buxifolia Ten.		×				
Subtribe Citrinae—						
Citropsis schweinfurthii S. and K.				×		
Poncirus (Citrus) trifoliata Raf.				×		
Atlantia citroides Pierre.		×				
Fortunella hindsii Sw.		×				
F. margarita Sw.	Nagami kumquat (oval).		×			
F. japonica Sw.	Marumi kumquat (round).	×				
F. crassifolia Sw.	Meiwa kumquat	×				
Citrus ichangensis Sw.		×				
C. medica Linn.	Corsican citron	×				
Do.	Etrog citron	×				
C. limonia Osbeck	Dwarf Chinese lemon				×	
Do.	Kenedy lemon					×
Do.	Lamb lemon					×
Do.	Rough lemon					×
Do.	Sweet lemon				×	
Do.	Villa Franca lemon					×
C. janos Tan.	Kansu orange	×				
C. aurantifolia Sw.	Kusaie lime					×
Do.	Mexican lime	×				
Do.	Persian lime	×				
Do.	Sour Rangpur lime					×
Do.	Tahiti lime			×		
Do.	Thornless lime	×				
Do.	Woglum lime	×				
C. grandis Osbeck	Conner grapefruit				×	
Do.	Davis grapefruit				×	
Do.	Duncan grapefruit				×	
Do.	Foster grapefruit				×	
Do.	Gold Medal grapefruit				×	
Do.	Hall (Silver Cluster) grapefruit.				[a] ×	
Do.	Leonardi grapefruit				×	
Do.	Marsh grapefruit				[b] ×	
Do.	Pink Marsh grapefruit				×	
Do.	McCarty grapefruit				×	
Do.	Pernambuco grapefruit.				×	

[a] More susceptible than most commercial varieties.
[b] Less susceptible than most commercial varieties.

TABLE I.—*Relative susceptibility of some rutaceous plants to citrus scab*—Contd.

Botanical name	Common or variety name	Range of susceptibility				
		No infection observed	Very rarely attacked	Slightly susceptible	Moderately susceptible	Very susceptible
Family Rutaceae—Continued.						
Subfamily Citratae—Continued.						
Tribe Citreae—Continued.						
Subtribe Citrinae—Con.						
C. grandis Osbeck	Royal grapefruit	×				
Do	Triumph grapefruit	×				
Do	Walters grapefruit				×	
Do	Chinese pummelo				×	
Do	Pink pummelo				×	
Do	Sour pummelo				×	
Do	Common shaddock				×	
Do. (?)	Cuban shaddock	×				
C. aurantium Linn	Bergamot orange	×				
Do	Bitter sweet orange					×
Do	Willow leaf bitter sweet orange				×	
Do	Myrtle leaf orange				×	
Do	Otaheite orange	×				
Do	Sour orange					×
C. sinensis Osbeck	Chamoudi orange	×				
Do	Florida Seedling orange		×			
Do	Enterprise orange	×				
Do	Homosassa orange	×				
Do	Jaffa orange	×				
Do	Lamb orange	×				
Do	Lue orange		×			
Do	Maltese orange		×			
Do	Mediterranean sweet orange		×			
Do	Norris early orange	×				
Do	Parson Brown orange	×				
Do	Pineapple orange		×			
Do	Ruby orange	×				
Do	Surprise orange	×				
Do	Valencia orange	×				
Do	Washington navel orange		×			
C. nobilis Lour	King orange					×
C. nobilis deliciosa Sw.	Clementine orange				×	
Do	Cleopatra mandarin	×				
Do	Dancy tangerine				×	
Do	Oneco tangerine				×	
Do	Mandarin				×	
C. nobilis unshiu Sw	Satsuma				×	
C. mitis Blanco	Calamondin					×
C. (Papeda) hystrix D. C.	Pointed leaf papeda				×	
Do	Round leaf papeda	×				
C. webberi Wester		×				
Microcitrus australasica Sw.	Australian finger lime	×				
Subfamily Toddalioideae—						
Tribe Toddalieae—						
Subtribe Toddaliinae—						
Toddalia lanceolata Lam.		×				

affected with scab on several occasions; while the Persian, which is very similar to the Tahiti, the Mexican, the Thornless, and the Woglum lime, appear to be immune.

Most grapefruit (*Citrus grandis*) varieties are only moderately affected by scab. The Hall appears to be more susceptible than most varieties, while the Marsh seems less likely to be seriously attacked, but this difference is not sufficiently great to justify separate spray schedules for these two varieties. The apparently immune Royal and Triumph varieties are regarded as hybrids of orange and grapefruit. On the other hand, the Leonardi variety, which possesses a number of the distinctive growth features of the Royal and Triumph, and which is considered by some to be an orange and grapefruit hybrid, is about as susceptible as most commercial varities of grapefruit. The pummelos are about as susceptible as most grapefruit. Scab has not been observed on the Cuban shaddock (considered by some to be a hybrid), a fact which increases

its potential value as a rootstock for nursery use, because scab has a marked stunting effect upon very young trees of susceptible varieties.

The Sour and Bittersweet oranges (*Citrus aurantium*) are severely attacked by scab; the varieties Myrtle Leaf and Willow Leaf are moderately attacked, but the disease has not been observed on the Bergamot and Otaheite forms.

The common or sweet Florida orange of commerce (*Citrus sinensis*) is highly resistant to scab. This species is affected so rarely that for all practical purposes it may be considered immune. A trace of scab has been observed a very few times on each of these following varieties—Florida Seedling, Lue, Maltese, Mediterranean Sweet, Pineapple, and Washington Navel. The diagnoses in these cases were verified by cultures from the affected parts. A scab-like blemish of undetermined cause has been observed occasionally on the sweet orange, but microscopic and cultural studies have consistently failed to reveal the scab fungus in the affected tissue.

The kid-glove oranges (*Citrus nobilis*) on the average at least, are as likely to develop scab as the grapefruit. The King variety is very susceptible, the Satsuma is distinctly less severely attacked, while the Cleopatra mandarin appears to be immune. Because of its immunity to scab and because it develops an excellent root system, the Cleopatra mandarin is gaining popularity as a rootstock in Florida.

The calamondin (*Citrus mitis*) is about as severely affected as the King.

The pointed-leaf form of Papeda (*Citrus hystrix*) is also severely attacked by scab, while the round-leaf form has not developed this disease.

Thus it seems that in the several groups susceptible to scab infection there is at least one commercial member on which scab occurs, though *Citrus sinensis* and *Fortunella margarita*, for practical purposes, are immune.

CITRUS HYBRIDS

Observations have been made on a rather large range of citrus hybrids and the degree of infection recorded for them is tentative and unless otherwise stated refers to leaf infections only. Many of these forms most likely will never be grown extensively, and only a few of them are now distributed through the citrus belt of Florida. For these reasons the relative susceptibility to scab can not be determined accurately at this time nor possibly in the near future. Table II gives the impressions gained from inoculations and numerous observations on the degree of scab infection on some citrus hybrids.

The data in Table II show that when both parents of the hybrid are attacked by scab the progeny in general is more likely to be affected by that disease than when only one parent is attacked, and a hybrid resulting from the crossing of two scab-resistant forms is likely to inherit the scab resistance of its parents. With but few exceptions, citrus hybrids are at least as severely attacked as the most susceptible parent. The only hybrid under observation with a scab-susceptible parent that has thus far been scab free is the Faustrimedin, a plant that does not resemble the Calamondin in any of its gross characters. It seems from the data in Table II that liability to scab attack is transmitted from susceptible parents to the first-generation progeny.

CITRUS SCAB OUTBREAKS

Citrus scab is very erratic in its outbreaks. Tender growth is the most highly susceptible. The outbreaks vary not only from season to season, depending on weather conditions, but with individual trees. The variation with different trees seems to be due to the fact that under Florida conditions a citrus tree may start growth as much as two weeks or more before the surrounding ones and even on one side of a tree new growth may sometimes be a week or more slower in starting than on the other. This disease also varies from district to district. The grapefruit and lemon in the Rio Grande Valley are affected by scab much less than in Florida. In Alabama the Satsuma and the Trifoliata orange are much more severely attacked than the same varieties are in Florida. Peltier and Frederich [6] report that in southern Alabama scab has not been observed on the Orangelo, Siamelo, or Siamor. The disease has been observed on these hosts in Florida. The Citrangequat seems to be more severely attacked in Alabama than in Florida.

The difference in degree of scab outbreak on a host in the several States seems more likely to be due to climatic conditions while the host is at a susceptible stage of growth rather than to fluctuating differences in inherent susceptibilities of the hosts or to altered virulence in strains of the pathogene.

[6] PELTIER, G. L., and FREDERICH, W. J. RELATIVE SUSCEPTIBILITY OF CITRUS FRUITS AND HYBRIDS TO CLADOSPORIUM CITRI MASSEE. Jour. Agr. Research 24: 955–959. 1923.

TABLE II.—*Relative susceptibility of citrus hybrids to citrus scab*

BOTH PARENTS SUSCEPTIBLE

Name of hybrid	Female parent	Male parent	C. P. B.[a] office numbers for hybrids	Range of susceptibility			
				No infection observed	Slightly susceptible	Moderately susceptible	Very susceptible
Citranguma	Citrus nobilis unshin Sw. (Satsuma)	Morton citrange	48055				×
Citremon	C. limonia Osbeck (Lisbon lemon)	Poncirus trifoliata Raf. (Trifoliata orange)	46163, 46219, 46356			×	
Citrumelo	C. grandis Osbeck (Bowen grapefruit)	do	4477		×	××	
Clemelo	C. grandis Osbeck (Duncan grapefruit)	Citrus nobilis delicosa Sw. (Clementine)	49851, 49859, 49862, 49866, 49910.			×	×
Do	C. grandis Osbeck (Bowen grapefruit)	do	49026, 49039, 49059			×	××
Do	C. nobilis delicosa Sw. (Clementine)	Citrus grandis Osbeck (Bowen grapefruit)	49933, 49941			×	××
Lemelo	C. grandis Osbeck (Chinese pummelo)	Citrus limonia Osbeck (Myers' lemon)	11045				×
Pomelolo	C. grandis Osbeck (Savage grapefruit)	Citrus grandis Osbeck (Marsh grapefruit)	40829			×	
Rangelo	C. aurantifolia Sw. (Rangpur lime)	Citrus grandis Osbeck (Sour pomelo)	52111			×	×
Satsumelo	C. nobilis unshin Sw. (Satsuma)	Citrus grandis Osbeck (Triumph grapefruit)	7270, 52022			××	
Do	do	Citrus grandis Osbeck (Bowen grapefruit)	52001, 52009, 52010, 52011.			×	×
Siamelo	C. nobilis Sw. (King orange)	do	50506, 50544, 51538, 51541, 51566, 51589, 51594, 51597, 51882, 51894, 51959, 51981, 51990, 52007, 52028, 52030.			×	×
Do	C. grandis Osbeck (Bowen grapefruit)	Citrus nobilis Sw. (King orange)	52013, 40104, 47043, 47044, 47047, 47075, 47286, 52013, 52015.			×	×
Do	C. nobilis Sw. (King orange)	Citrus gradis Sw. (Duncan grapefruit)	44368			×	×
Sopodia	C. grandis Osbeck (Sour pomelo)	Citrus aurantium Linn (Sour orange)	52038			××	
Soporin	C. nobilis Sw. (King orange)	Citrus grandis Osbeck (Sour pomelo)	51289, 51310, 51519, 51524.			×	×
Tangelo	C. grandis Osbeck (Bowen grapefruit)	Citrus nobilis delicosa Sw. (Tangerine)	52016, 52018				××
Tangelo, Sampson	Grapefruit	Dancy Tangerine	7140				×××
Tangelo, Sampson seedling	Grapefruit	Dancy Tangerine					×××
Tangelo, Thornton	Second generation of Sampson seedling		L-762, L-765				××
Tangelo, Webber	Citrus grandis Osbeck (Savage grapefruit)	Tangelo	40969				××
Tangelolo	do	Sampson tangelo	47206, 47207, 47214, 47220, 47222.				××
Do	C. grandis Osbeck (Bowen grapefruit)	Tangelo	52014				×
Tangelorin	C. nobilis Sw. (King orange)	do	51106, 51115				××

[a] Office of Crop Physiology and Breeding Investigations, Bureau of Plant Industry, U. S. Department of Agriculture

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TABLE II.—*Relative susceptibility of citrus hybrids to citrus scab*—Continued

ONE PARENT SUSCEPTIBLE AND ONE RESISTANT

Name of hybrid	Female parent	Male parent	C. P. B. office numbers for hybrids	Range of susceptibility			
				No infection observed	Slightly susceptible	Moderately susceptible	Very susceptible
Citradia	Poncirus trifoliata Raf. (Trifoliata orange)	Citrus aurantium Linn (Sour orange)	50049			×	
Citrage, Rusk	do	Citrus sinensis Osbeck (Seedling orange)	11540		×	×	
Citrage	Citrus sinensis Osbeck (Washington navel)	Poncirus trifoliata Raf. (Trifoliata orange)	45152, 45169, 45174		×	×	×
Citragequat, Thomasville	Fortunella margarita Sw. (Oval kumquat)	Willits citrange	48010		×		
Faustrimedin	Microcitrus australasica Sw. (Australian finger lime)	Citrus mitis Blanco (Calamondin)	47431	×			
Lemonime	Citrus aurantifolia Sw. (Mexican lime)	Citrus limonia Osbeck (Genoa lemon)	48848			×	
Lemonquat	C. limonia Osbeck (Genoa lemon)	Fortunella margarita Sw. (Oval kumquat)	48770			×	
Limelo	C. aurantifolia Sw. (Mexican lime)	Citrus grandis Osbeck (Sour pummelo)	47123			×	
Do	C. aurantifolia Sw. (Rangpur lime)	do	52111			×	
Orangelo	C. grandis Osbeck (Bowen grapefruit)	Citrus sinensis Osbeck (Parson Brown orange)	40952			×	
Do	do	Citrus sinensis Osbeck (Lamb's summer orange)	49078, 49178			×	
Do	do	Citrus sinensis Osbeck (Ruby blood orange)	47022			×	
Siamor	C. nobilis Sw. (King orange)	do	52029				×

BOTH PARENTS RESISTANT

Faustrime	Citrus aurantifolia Sw. (Mexican lime)	Microcitrus australasica Sw. (Australian finger lime)	49810, 49823	×			
Limequat	do	Fortunella japonica Sw. (Round kumquat)	48798	×			

PARENTAGE NOT FULLY KNOWN

Lemon hybrid	Probably Citrus limonia Osbeck (lemon) and Citrus medica Linn. (citron)		S. P. I. No. 23367[b]				×
Microcitrus hybrid	Probably Microcitrus australasica Sw. (Australian finger lime) and Microcitrus australis Sw. (Dooja lime)		7775	×			
Natsumikan	Probably Citrus grandis Osbeck (Pummelo) and Citrus nobilis Sw		11184, 11337		×		
Tangelo			S. P. I. No. 19610[b]				×
Tangelo ? Wales							×
Temple	Orginal tree, parents unknown						×
Do	Bud progeny		11159				×
Do	Seedling						×

[b] Office of Foreign Seed and Plant Introduction, Bureau of Plant Industry, U. S. Department of Agriculture.

SUMMARY

The citrus scab fungus attacks a comparatively narrow range of plants in the family Rutaceae, as indicated by observations and inoculations made on 2 subfamilies, 2 tribes, 4 subtribes, 22 genera, 35 species, 71 varieties, and 47 hybrid combinations. Many citrus forms appear to be immune, while the susceptible ones exhibit all grades of resistance.